THE INFLUENCE OF MICROSITE AND SEED LIMITATION ON ANNUAL WEED SEEDLING RECRUITMENT IN ARABLE AGRICULTURE

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ABSTRACT

The germination and emergence of a seedling, or seedling recruitment remains an essential process in the establishment of a plant. This establishment can be limited by the availability of microsites within the soil profile, or the availability of seed within a given area. Three field experiments were initiated in Saskatchewan, Canada to examine the relative effect of seed and microsite limitations on weed seedling recruitment. The first experiment examined the effect of landscape position as well as nitrogen (N) rate and tillage system (zero tillage vs. conventional tillage) on weed seedling recruitment from an indigenous weed population. Survey results indicated habitat differentiation of the weed population with wild oat and cleavers preferentially recruiting in the lower landscape positions, Russian thistle and Kochia in the upper landscape positions, while green foxtail recruited in high levels on all landscape positions. This suggested that different weed species have different microsite requirements for weed seedling recruitment across contrasting landscape positions. The second field experiment examined the effect of landscape position and moisture availability on weed seedling recruitment from an artificial hand-seeded weed seedbank. This experiment indicated that seed limitation remained a very important factor, but even when irrigated, total seedling recruitment did not reach maximum recruitment, indicating water was not the only limiting resource for weed seedling recruitment. Microsite limitations were greatest on the upper slope position for all species with green foxtail having the greatest overall recruitment of the species across all landscapes and moisture regimes. The third experiment examined the effect of tillage system and density on weed seedling recruitment of wild oat, green foxtail, and wild mustard. Again, weed seedling recruitment remained a function of both microsite and seed limitations as absolute recruitment values increased for each density examined in this experiment. The agronomic significance of microsite limitation was negligible as high weed population numbers occurred for the highest weed seeding densities. Overall, microsite limitations

remained negligible in these experiments for arable agriculture with the main influence on weed seedling recruitment most often being seed limitation in the natural seedbank.

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1. Introduction

Despite widespread acceptance of herbicide use in western Canada, weed species and populations continue to persist in arable agriculture. Our ability to control weeds by herbicide methods has significantly reduced our knowledge on the basic biology of weed species. There is a need to have a greater understanding on the persistence, germination, emergence, growth, and reproduction of weed species in arable agriculture to better assess the complexity of weed populations found across western Canada. Increased knowledge on the biology of weeds may decrease pesticide use by predicting future populations of a weed prior to establishment in an area.

Within the biology of weeds, seedling recruitment, which is defined as the establishment of a seedling from a seed via germination and emergence (Harper, 1977), remains a crucial preliminary step in establishing a plant into a community for the majority of ecosystems. Seedling recruitment is limited by the availability of seed or availability of a favourable microsite. A microsite is a small-scale site surrounding the prospective seed that immediately affects a seeds ability to proceed in both germination and emergence (Eriksson and Ehrlen, 1992). The microsite concept evolved from the 'safe-site' concept termed by Harper (1977). A safe-site is a small-scale site specific to each species and must contain a stimulus to break dormancy, conditions necessary for germination to occur, resources (water and oxygen) that are consumed by the seed during germination, and freedom from hazards such as insect and diseases before seedling recruitment will occur. Knowledge on the microsite requirements of a species may allow prediction of both the population of weed species in an environment as well

as the specific species that will recruit into specific areas of the field. Despite the ecological introduction of the microsite concept over 25 years ago, its relative importance in arable agriculture has largely been ignored. Understanding the relative influence of microsites on successful recruitment of a number of annual weed species will increase our basic understanding of why weeds establish and dominate in patches within the landscape.

Key questions addressed by this thesis will revolve around the relative importance that microsite and seed limitations have on weed seedling recruitment in arable lands. In agriculture, the most obvious example of apparent microsite limitations is observed on hummocky glacial till fields across western Canada with the majority of weeds observed to be located in the lower landscape positions. Despite these observations, the question remains whether the difference in weed presence across variable landscapes is due to microsite variability or the availability of seed. What is the most limiting factor in weed seedling recruitment of annual weed species and is seedling recruitment the most important step in the development of weeds in patches? Are there weed species that prefer upper slope positions because the are better adapted to succeed in this environment or are their microsite requirements are greater fulfilled?

Additionally, by manipulating the microsite with the addition of water or tillage, one can examine if differences in the environment or management practices result in differential seedling recruitment of weed species and thereby determine potential microsite characteristics for a number of annual weed species. This thesis will examine the influence of microsite limitation and seed availability on the overall spatial distribution of weeds in arable agriculture. Findings from this thesis will increase our knowledge on the biology of weeds and give us a better understanding of the spatial

patterns of weeds within all agricultural fields. Ultimately, we hypothesize that weed seedling recruitment is limited in arable agriculture by availability of microsites.

2. Literature Review

2.1 Limitations on Weed Seedling Recruitment

Successful seedling recruitment is the essential preliminary process in the establishment of a species in an environment. The ability of a species to favourably recruit within an area is dependent upon two things: the availability of seed and the availability of favourable microsites. A microsite is a small-scale site surrounding the prospective seed that immediately affects a seed's ability to proceed in both the germination and emergence processes (Eriksson and Ehrlen, 1992). Seed limited recruitment occurs when the number of seeds in the soil limits recruitment, despite having more than enough favourable microsites.

The relative importance of microsite and seed limited recruitment has been examined mainly in natural ecosystems (Eriksson and Ehrlen, 1992; Bisigato and Bertiller, 1999; Maron and Gardner, 2000; Turnbull et al., 2000; Juenger and Bergelson, 2000; Coulsen et al., 2001; Strykstra et al., 2002). In ecosystems with increased disturbances such as fire, deforestation and grazing, seed limitation tends to be more dominant than microsite limitation as disturbance increases the available microsites for the available seeds within the soil profile (Crawley, 1990; Eriksson and Ehrlen, 1992; Eriksson, 2000; Maron and Gardner, 2000; Cummings and Alexander, 2001). Considering seedling recruitment is an essential first step in plant establishment, the relative importance of microsite and seed limitation remains to be explored for weeds of intensively managed agricultural fields (Crawley, 1990). In experiments where disturbance is utilized to increase seedling recruitment, no strict dichotomy of seed vs.

microsite limitation in plant population regeneration is observed (Juenger and Bergelson, 2000). In a recent review of seed augmentation experiments, approximately 50% of experiments in natural settings have seed limited recruitment (Turnbull et al., 2000); however, there was a general lack of information on agricultural or ploughed fields.

Using grasslands as an example, newly broken land exhibited seed limited recruitment, but seedling recruitment increased over time as weeds infested an area (Chancellor, 1985). As a result, the entire weed population can increase and in this example the weed population increased from 29 weeds m^{-2} to 196 weeds m^{-2} after twenty years of continuous cropping. This increase in total plant density occurred simultaneously with a decrease in diversity as grassland weeds were eliminated over time, perhaps losing their microsite for successful seedling recruitment. In addition, the aggregation of microsites along a grassland landscape may be more important than competition in determining the ability of a plant to recruit and survive, as seeds close to neighbouring plants have a greater chance of survival (Fowler, 1988; Tofts and Silvertown, 2000).

2.1.1 Significance of seed and microsite limitations in arable agriculture

In agricultural fields, the weed seedbank allows for a species to persist over time providing a constant presence for successful weed seedling recruitment (Rees, 1996). The presence of long-lived seedbanks allows different species to emerge due to the temporal changes in the environment (Rees and Long, 1992). Weed seedbanks can be quite substantial and variable with estimates of total seedbank numbers of 16,000 total weed seeds m^{-2} for cultivated agricultural lands (Forcella et al., 1993) to 80,600 green

foxtail seeds m^{-2} alone in cultivated agricultural lands (Spandl et al., 1998) for two experiments in Minnesota.

As weed seedbanks mature over time, only a few weed species remain persistent in high quantities. From these seedbanks, only a fraction of weed seeds germinate each year, ranging from 9.0 to 28.1% (Dessaint et al., 1997) with the maximum annual emergence being approximately 40% (Forcella, 1992). For individual species, such as wild oat, recruitment from the seedbank can be as high as 60%, due to its relatively short-lived seedbank (Medd, 1996) and as low as 2.5% for wild mustard with a long-lived seedbank (Edwards, 1980).

In some cases, agricultural seedbanks exhibit significant similarities between the seedbank and seedling populations (Cavers and Benoit, 1989; Dessaint et al., 1997), indicating that under ideal conditions, a prediction of the weed flora based on seedbank availability and microsite requirements for each species should be possible. Unfortunately, simply sampling the seedbank is not a good determinant of future seedling populations for site specific management as interactions between indigenous weed populations and soil conditions or management result in different weed populations between fields (Cardina et al., 1996; Derksen et al., 1998). As an example, with similar abundance in the seedbank, 0.1% of lambsquarters emerged in zero-tillage while 38% of grasses emerged illustrating the soil seedbank is only one factor in determining the resulting weed population (Cardina et al., 1996). The microsite requirements of the species must have an influence on the resulting weed flora.

2.1.2 Factors that influence microsite limitation

A microsite is characteristic for individual species with the conditions that result in one species to recruit may be unsatisfactory for another. Classical experiments in manipulation of the microsite have illustrated varying the water supply to a sintered glass plate can affect overall germination. Varying the osmotic potential will result in different germination responses due to different microsite requirements (Harper and Benton, 1966). In addition, the roughness of the soil influenced microsite requirements of species as smooth surface soils favoured *Bromus rigidus* recruitment while rough textured soils favoured *Bromus madritensis* recruitment. The difference in recruitment was attributed to the embryo of *B. madritensis* remaining in the air on smooth soils, thus limiting successful recruitment (Harper et al., 1965). Texture and strength of the soil surface may also restrict successful seedling recruitment, as some species cannot penetrate the crust that can form on the soil surface (Stolzy and Barley, 1968).

Soil heterogeneity through soil aggregation creates a variety of microsites with different moisture and aeration conditions, which may regulate seed germination and seedling establishment (Harper et al., 1965; Evans and Young, 1972). In zero-tillage or reduced tillage systems, there are less weed seeds inside soil aggregates (Pareja et al., 1985). The conditions inside and outside a soil aggregates differ with oxygen limitation inside the aggregates (Currie, 1965) and water limitation outside the aggregates predominating (Pareja and Staniforth, 1985).

Weed populations in the soil are composed of several sub-populations occupying different seed-soil microsites, with smaller seeds unable to germinate from larger soil aggregates and surface weed seeds limited by the availability of moisture before evaporative water loss dries out the germinating seed (Pareja and Staniforth, 1985).

Seeds often are found in soil aggregates larger than 9 mm with the highest seed viability found in aggregates that are closest to the seed size (Reuss et al., 2001).

The presence of a litter layer over the soil surface may determine the microsite requirements of a species as an increase in litter can result in decreased seedling recruitment. Litter can also decrease the overall biomass of weeds, affecting plant fecundity, reducing the plants ability to reproduce for future generations of a population (Molofsky et al., 2000). For weed species germinating through a mulch layer, regardless of the type of mulch, different sensitivities to seedling emergence result in seedling recruitment of plants that are able to grow around obstructing objects (Teasdale and Mohler, 2000).

Depth in the soil is another factor that will limit seedling recruitment based on individual species microsite requirements. Wild oat germinating from 6 cm or deeper have significantly reduced emergence due to mortality by microbial attack when compared to sterilized soil, but no difference from the 1 cm depth (Pickering and Raju, 1996). Maximum depth of recruitment is species specific with a 14.5 cm maximum depth for wild oat and 9.0 cm maximum observed depth for green foxtail in a recent study (Du Croix Sissons, 2000).

Seed size can affect the microsite requirements for different species as well as the rate of germination. The rate of germination can be important under conditions of high evapotranspiration, where moist soils can dehydrate rapidly (Gealy et al., 1994). Larger *Brassica napus* seeds can emerge from a wider range of soil substrates than smaller *Raphanus sativus* seeds (Harper, 1977). In general, smaller seeds tend to emerge at an increased rate from shallow depths, but larger seeds have a higher rate of emergence from deeper soil depths (Harper and Obeid, 1967). This is likely due to the

availability of resources within the seed that allow for larger seeds to emerge from greater depths. Although germination percentage may be similar between species with different seed sizes, a greater number of seedlings from larger seeds survive in nature, while the smaller seeded species occupy the spaces where larger seeded individuals are limited by the availability of seed (Turnbull et al., 1999; Eriksson, 2000). Thus, small, highly dispersed seeds may be more limited by microsites than large, low dispersed seeds that are mainly limited by availability of seed (Eriksson, 2000).

Species-specific moisture and temperature requirements determine the ideal microsite for a species with different species germinating under contrasting conditions. For *Malva pusilla* emergence, soil moisture has a greater effect than soil temperature (Blackshaw, 1990), while *Anthemis cotula* needs both high temperature and moisture for successful recruitment (Gealy et al., 1994). Seeds of *Campis radicans* need a temperature of 30/20^{o}C day/night temperature with an osmotic stress no less than -0.2 MPa before germination will occur (Chachalis and Reddy, 2000). Forcella (1998) indicated soil temperature is the most important ecological variable for soil-borne seeds and seedlings before they reach the soil surface but emergence will cease on days where soil water potential falls below threshold values specific to each species. Between similar species, *Avena fatua* has increased recruitment in soil temperatures greater than 20^{o}C, while *Avena sterilis* has increased recruitment from soils less than 10^{o}C (Fernandez-Quintazilla et al., 1990). *Setaria viridis* has a decreased rate of emergence under both dry soil conditions and low temperatures, but will emerge at the same time as wheat under warm, moist conditions (Blackshaw et al., 1981) as well as under increased temperatures indicative of global warming experiments (Lee et al., 2001). Base temperatures will determine whether a species will be able to germinate within a specific

time frame. Each species has a characteristic base temperature for germination with a 0.35 to 1°C base temperature for *A. fatua* (Fernandez-Quintazilla et al., 1990; Cousens et al., 1992), and a 4.4 to 10°C base temperature for green foxtail (Douglas et al., 1985).

Microsites can differ in terms of pH and different species may preferentially recruit under specific pH conditions. Most species will recruit in a pH between 5 and 9 with minimal or no germination at a pH of less than 4 or greater than 10 (Chachalis and Reddy, 2000).

Seedling recruitment can also be limited by the availability of light penetrating a canopy thus allowing germination only under optimal conditions for successful survival without competition for available resources (Hazebroek and Metzger, 1990; Reader and Buck, 1986). Detection of gaps due to light quality and temperature can promote weed species to germinate (Aldrich, 1984; Benech Arnold et al., 1988), only recruiting after satisfying microsite requirements.

It is evident that there are numerous factors that restrict seedling recruitment of all species in the same environment. Both the availability of microsites and seed will limit the potential of agricultural weed species to recruit. It is important to determine the main environmental and physical factor limiting recruitment. By conducting experiments under a variety of environments and soil conditions for a number of weed species, we will better understand the biology behind weed seedling recruitment of specific weed seedlings.

2.2 Seedling Recruitment

2.2.1 Annual weed seedling recruitment in the agroecosystem

Harper (1977) described the life cycle of a plant from seed germination and emergence to reproduction and seed set as a series of stages termed the environmental sieve. At each stage of life a plant has obstacles such as predation, resource limitation, competition, etc. that limits further development or can result in possible death. As a plant passes through the environmental sieve, the most critical stage is seed survival through germination and emergence of a seedling or seedling recruitment (Harper, 1977; Schupp, 1995). If the soil is made up of a series of microsites filled with seeds, two seeds occupying the same microsite will compete against one another for successful recruitment and ultimately the larger more competitive seed will win due to increased competitive ability of the seedling (Turnbull et al., 1999). Small seeded individuals remain within the landscape as many times the larger species are limited by seed number and do not fill all available microsites (Turnbull et al., 1999).

Species response to environmental conditions are different with weeds such as wild oat recruiting early while green foxtail will tend to recruit after crop emergence (Blackshaw et al., 1981; Douglas et al., 1985). Agricultural lands are subject to intense disturbances with high resource availability and low plant densities. As a result, there are many open sites for successful weed seedling recruitment. In addition, weed seed production is relatively high per plant, even with the use of herbicides; therefore, weed seedling recruitment is hypothesized to be rarely limited by the number of propagules (Ghersa and Roush, 1993).

The weed flora, although in relatively stable spatial patterns, will shift composition over space and time in response to climatic and cropping variations

(Forcella and Harvey, 1983; Radosevich et al., 1997; Fround-Williams 1988). Seedling recruitment is buffered between years by the existence of various mechanisms of dormancy or safe site protection for species to germinate and emerge over an extended period of time (Zimdahl, 1999). Ultimately, seedling recruitment tends to be heterogeneous across a field with distinct patches occurring (Schupp, 1995).

Despite the fact that seedbank numbers can be substantial, maximum seedling recruitment numbers determined using survey data remain relatively low (Leeson et al., 2003). Although surveys typically are performed after herbicide application, maximum infestations should illustrate a level of maximum potential seedling recruitment within a field. This maximum survey infestation level is potentially lower than actual seedling recruitment due to self-thinning of weed species before the survey timing. Maximum density observed in Saskatchewan was 487.8 plants m^{-2}, 248 plants m^{-2}, and 37.4 plants m^{-2} for green foxtail, wild oat, and wild mustard, respectively (Thomas et al., 1996). Although these numbers are quite substantial, maximum seedbank densities have been estimated at 16,000 weed seeds m^{-2} (Forcella et al., 1993) or 80,000 green foxtail m^{-2} (Spandl et al., 1998). The observed numbers are significantly less than 100% recruitment from the seedbank. Even under less herbicide use in the late 1970s, with increased available moisture in Manitoba, maximum densities were 2638.2 plants m^{-2}, 922.2 plants m^{-2}, and 186.8 plants m^{-2}, for the same three species (Thomas and Donaghy, 1991). Although seed limited recruitment is evident in many agricultural fields with low seedbank numbers, the relative importance of microsite and seed limitation on maximum plant densities is largely undetermined.

2.2.2 Factors influencing seedling recruitment

2.2.2.1 Disturbance/Tillage effects

Any form of disturbance can have a profound influence on the successful seedling recruitment of individuals in a population. In a woodland ecosystem, recruitment was highest in the most disturbed clear-cut area as opposed to a rocky or herbaceous area (Owens et al., 1995). Disturbance by clipping in grassland swards had a positive effect on 16 of 45 species that had previously exhibited seed limited recruitment with a greater influence on small-seeded species (Jakobsson and Eriksson, 2000). For perennial species, disturbance by clipping along with seed addition will increase overall recruitment when compared to control plots with no disturbance and seed addition, but not by seed addition or disturbance alone (Juenger and Bergelson, 2000). Increased grazing with the addition of seed to the bunchgrass *Themeda triandra* will encourage seedling recruitment much more than ungrazed, undisturbed grasslands (O'Connor, 1996).

Depending on the year, study, and species, a tillage treatment can have a positive, negative, or neutral effect on annual weed seedling recruitment. With the introduction of zero-tillage systems in western Canada, many studies have examined the population changes through time as practices shift from a conventional tillage or chisel plough tillage system to a minimum disturbance system where the only cultivation practice occurs with the seeding implement. Cultivation encourages many weeds to germinate and has stimulated wild oat emergence when the cultivation procedure occurs at the timing of germination (Banting, 1966). Emergence of added seeds can be increased by 1.5 to 3 times with cultivation (Peters, 1991). As well, with this increased recruitment, the seedbank is depleted at a more rapid pace with no viable seeds

remaining at the end of three years compared to 3% viable seeds remaining in a zero-tillage treatment (Peters, 1991).

Green foxtail has a greater emergence from the upper 1cm of soil as tillage decreased, which is to be expected as a greater proportion of the seeds are in the upper portion of the soil profile (Buhler and Mester, 1991). The shift in cropping system from the mouldboard plough to zero-tillage and chisel plough has also resulted in increased green foxtail recruitment as weed seeds remain in the upper portion of the soil where successful weed seedling recruitment is possible (Ball and Miller, 1993; McGriffen et al., 1997; Spandl et al., 1998). Depending on the year, green foxtail can have higher (Spandl et al., 1998) or lower emergence in zero-tillage (Spandl et al., 1999) with the difference between years attributed to soil temperature. Greater prediction of soil moisture and temperature can be obtained for a mouldboard plough system. The prediction of seedling recruitment based on tillage type and species proves to be very difficult in the more variable chisel plough or zero-tillage system compared to mouldboard plough (Spandl et al., 1999). With more moisture, the effect of tillage on green foxtail recruitment is exaggerated as an increase in emergence with soil disturbance can increase approximately 6-fold (Mulugeta and Stoltenberg, 1997); even without added moisture, green foxtail densities can increase five-fold in chisel plough in comparison with mouldboard plough (McGriffen et al., 1997).

Conversely, if zero-tillage systems can maintain the weed species on the surface, there can be a reduction in seedling recruitment as surface seeds have lower recruitment than seeds that are buried by a tillage treatment (Anderson et al., 2002). For seedling recruitment to be minimized in a no-tillage operation there must be minimal soil disturbance at the time of seeding.

In other studies there is no difference between the total weed population in comparing zero-tillage, conventional, and reduced tillage systems (Derksen et al., 1994). The main difference is not the absolute number of species present, but the shifts in weed communities (Derksen et al., 1994). There is a shift in the weed community in zero-tillage to increased grasses, wind dispersed individuals, perennials, and volunteer crops (Swanton et al., 1993).

Increases in seedling recruitment with a no tillage system tend to be due to the species that persist within that system. Those species that can germinate from shallow depths tend to be small seeded species (Koskinen and McWhorter, 1986). No tillage favours weeds such as kochia and Russian thistle (Koskinen and McWhorter, 1986; Anderson et al., 1998), along with the foxtail species (Anderson et al., 1998). In contrast, higher wild mustard and lambsquarters occurred under conventional tillage systems (Anderson et al., 1998); however, under drought years, cultivation reduced the number of wild mustard plants surviving to maturity (Edwards, 1980), thus affecting the fecundity of the species. Wild oat is another species that has the ability to emerge from greater depths and is favoured in a conventional tillage system (Pickering and Raju, 1996). Again, water stress throughout the growing season will reduce the fecundity of the wild oat (Peters, 1982), which may be exacerbated by the cultivation procedure. In general, all annual weed species are favoured in recently cultivated land, no matter the method of cultivation (Stolcova, 2001). Deep tillage reduces the ability to emerge and most species, including wild oat, will have almost no seedling recruitment from below the 15cm depth (Navarette and Fernandez-Quintanilla, 1996).

2.2.2.2 Nutrient/Soil property effects

Both differences in soil properties and nutrient supply will result in differing levels of seedling recruitment with seedling recruitment being promoted under more beneficial environments. Communities become more susceptible to invasion by a weed species whenever there is an increase in the availability of unused resources (Davis et al., 2000). In both natural communities and agricultural communities, soil nutrients are strongly associated with the organic matter composition of the soils. Characteristic changes in the vegetation result from changes in organic matter and water holding capacity of the soil (Pregitzer et al., 1983; Andreasen et al., 1991). Agricultural lands are susceptible to invasion due to the addition of nutrients and the continuous disturbance created by seeding, herbicide, tillage operations, and the yearly removal of crops.

Soil moisture and temperature are two factors that will affect seedling recruitment from year to year with some species more susceptible to osmotic stress or moisture deficit than other species (Fernandez Quintanilla et al., 1990). Soil temperatures with adequate moisture will determine the timing of seedling recruitment as increased temperatures will allow weeds such as green foxtail to successfully recruit with the crop as opposed to delayed recruitment under cooler soil conditions (Blackshaw et al., 1981).

The addition of nitrogen by inorganic fertilizers has been examined with respect to successful weed seedling recruitment. The addition of fertilizer not only increases the ability of a species (e.g., grasses) to out-compete other individuals (e.g., Canada thistle (*Cirsium arvense)*) due to differences in need for nutrients (Edwards et al., 2000) but it also affects the seedling recruitment of many species. Weeds such as lamb's quarters

(*Chenopodium album*) and Nettle species (*Lamium* spp.) have a lower nitrogen optimum than a crop such as barley (*Hordeum vulgare)* for successful germination and establishment, while *Urtina urens* has a higher N optimum (Jornsgard et al., 1996). This results in different weed flora depending on the nitrogen treatment. Addition of nitrogen has resulted in increases in germination (Williams and Harper, 1965; Agenbag and Villiers, 1989; Kirkland and Beckie, 1998), no difference in weed germination (Jornsgard et al., 1996), as well as decreases in total seedling recruitment with nitrate addition up to 448 kg N ha^{-1} (Fawcett and Slife, 1978). In cases where there was no difference in weed seedling recruitment, the weed density decreased through time due to increased competition by the crop with adequate nitrogen rates (Jornsgard et al., 1996).

Broadcast application of fertilizers can greatly increase the emergence of weed species, such as wild oat and broadleaf weeds, but the increase in fertility tends to be detrimental to green foxtail as crop competition limits successful seedling recruitment of later emerging weed species (Kirkland and Beckie, 1998). In sandy and loamy soils, the addition of any form of ammonium nitrate fertilizer increased seedling recruitment of wild oat by 25 to 35% in comparison to no fertilizer (Agenbag and Villiers, 1989). To limit the increases in weed seedling recruitment by fertilizer application, band seeding of nitrogen with the crop does not increase seedling recruitment and ultimately decreases the fecundity of the weed species as the crop utilizes more of the supplied nutrients (Berkowitz, 1988; Kirkland and Beckie, 1998; Scursoni and Arnold, 2002). As a consequence, a zero nitrogen treatment often results in the greatest reproductive output per weed due to decreased emergence and intraspecific competition of weed species (Jornsgard et al., 1996). Even when weed growth is reduced due to decrease in fertility, there is an increase in reproductive allocation of individual plants compared to larger,

highly fertilized treatments, maintaining high fecundity under stress and maintaining a constant and high weed seed production to the weed seedbank (Jackson and Somers, 1991; Sugiyama and Bazzaz, 1997).

Associations between soil textural classes and weed species dominance in an area have been examined. Wild mustard has been found to have increased frequency with increasing clay content in the soil (Andreasen et al., 1991), as well as *Stellaria media* (Walter et al., 2002). In contrast, *Viola arvensis* had a negative association with clay content in the soil (Walter et al., 2002). Unfortunately, the relationship between weed densities and soil properties tends to be field specific (Heisel et al., 1999).

2.2.2.3 Landscape effects

The effect of landscape and differences in its productivity for crops has been extensively examined in agriculture and many inferences on the effect of seedling recruitment can be made based on productivity along contrasting slope positions. Nonetheless, crop yield and productivity may not mimic weed seedling recruitment. Topography influences the redistribution of soil particles, organic matter, and soil nutrients, resulting in characteristic changes in both the chemical and physical properties along slope positions (Pennock and de Jong, 1990). Even subtle variation in topography can result in a significant variation in soil properties (Pennock et al., 1987; Pennock et al., 1992). Much of the differences in weed seedling recruitment along the slope positions could be a result of these different soil properties within the landcape. Yield of both crops and the weed flora are correlated to both the slope position and organic matter content of the soil with a large range in yield under dry conditions from lower to upper slopes and relatively uniform yields in above average years (Kravenchenko and

Bullock, 2000). In a study conducted on hummocky glacial till landscape in Saskatchewan, water content differences in slope positions were greatest during the wettest years (Walley et al., 2001). Increased rainfall results in increased accumulation of water in the lower landscape positions.

Between years, the total seedling recruitment of individuals can be significantly different due to environmental factors. With above average precipitation, the lower landform element complexes can exhibit high wild oat and hemp nettle densities, but in the same field under normal precipitation, this is not observed (Manning et al., 2001). Additionally, erosional surfaces like those expressed on the upper landscape positions, can decrease the productivity within a landscape up to 89% (Geiger and Manu, 1993), amplifying the effect of moisture deficit on upper slope position productivity. In contrast, under some circumstances, the best habitat for emergence of species is at the top of knolls due to availability of bare soil for successful recruitment (Reader and Buck, 1986). The increased light interception at the bottom of depressions by a crop canopy will result in a reduced ability of certain late emerging weed species to emerge (Reader and Buck, 1986).

Predation of seed can have an effect on weed seedbank abundance, especially when seed sits on soil surface in a zero tillage situation. Studies indicate a lower predation of seeds in simplified agricultural landscapes than in more complex landscapes (Menalled et al., 2000). Concentrated removal of weed seeds in a landscape position, such as a lower landscape could have marked effects on potential weed seedling recruitment; however, much of the effects are buffered by immigration of weed seeds by dispersal (Menalled et al., 2000). In many cases, a large change in the seed predation

rate in complex landscapes may have no measurable effect on weed seedling recruitment (Crawley and Nachapong, 1985).

2.3 Weed Patch Dynamics

2.3.1 Characterizing weed patchiness

The ultimate goal of characterizing weed seedling recruitment is the ability to predict the emergence of weed species within a field. Microsite and seed limited recruitment results in differential weed seedling recruitment with weeds being aggregated rather than distributed uniformly within fields (Palmer, 1992; Moloney and Levin, 1996; Gerhards et al., 1997; Dale, 1999; Clay et al., 1999; Dieleman et al., 2000: Colbach et al., 2000b). Weed monitoring methods, although an important first step in determining weed patch dynamics, have a low predictive value because they tend to be descriptive in nature (Fernandez-Quintanilla, 1988). Many of the methods involve intensive weed sampling at various scales and the use of mathematical interpolation techniques such as linear triangulation (Gerhards et al., 1997), polynomial interpolation (Zanin et al., 1998), or kriging (Colbach et al., 2000a) to generate maps. The scale of the sampling procedure limits these methods. Often, interpolation methods cannot account for dense weed patches because sampling size is just too large and infeasible at a small scale (Rew and Cousens, 2001). Because weeds are in multi-species assemblages that shift in composition, dominance and density in space and time (Van Groenendael, 1988), it is important to describe how weed species change as a result of various environmental and management influences (Auld and Coote, 1990; Colbach and Debaeke, 1998). The lifecycle of weed species needs to be broken down into the various stages of plant growth and development, and analyzed individually with the goal of

establishing functional relationships between the biological and environmental factors that influence plant development (Fernandez-Quintanilla, 1988). This mechanistic understanding of the causes of spatial variation of weed patches needs to be established (Dieleman et al., 2000).

2.3.2 Predicting weed patches

Numerous models have been developed to aid in prediction of future weed patches with varying degrees of complexity and success. By producing comprehensive models based on the biology of seedling recruitment, the ability to predict future patches of weeds will aid in developing site-specific management practices for farmers.

Some models have been developed independent of any soil or environment factors to illustrate that clusters of weeds tend to remain in the same spot over several years (Wallinga, 1995), which has been observed in some fields (Dessaint et al., 1997; Johnson et al., 1996). As farmers try to maintain weed densities at the lowest possible levels, Wallinga (1995) illustrated, with weed control efforts, that only a few offspring disperse away from the center of the cluster, as the highest probability of survival is located in the center of the weed cluster.

Simulation models trying to connect tillage systems with potential weed seedling recruitment indicate that temperature and moisture conditions for the seed are easier to predict under a no-tillage system (Oryokot et al., 1997). There appears to be greater predictability for seedling emergence of pigweed species (*Amaranthus* spp.) in comparison to mouldboard plough because the heterogeneity of weed seed distribution within a cultivated soil decreases a models' ability to predict seedling recruitment in

comparison to a zero-tillage system where weed seeds are located at or near the soil surface (Oryokot et al., 1997).

Models which incorporate microsite limited recruitment tend to indicate competitive exclusion is more important than microsite. Landscape complexity and environmental variability will allow for species to coexist, as there are almost no microsites where a single species performs at its optimum (Palmer, 1992). Instead, there is a range of good and poor microsites within a given landscape complex and species only persist in an environment where reproduction is favoured. Nearby sites will be favourable for the same species indicating there is a spatial dependence and independence of microsites in any given location (Palmer, 1992). Another model that examines the possibility of microsite vs. seed limitation incorporates the possibility of using the meta-population theory for the exploitation of species in temporary habitats (Van der Meijden et al., 1992), but their applicability to agricultural fields is negligible.

Mechanistic or empirical models attempt to examine on-site properties, such as elevation, percentage organic matter, nitrate, pH, phosphate, and soil texture with knowledge of the previous years weed data to predict future patch dynamics of species (Dieleman et al., 2000). Although these methods can work for a field specific management, the parameters used in the model often differ between fields, even in the same geographic area due to field specific management practices (Johnson et al., 1995). Often, the lack of a climatic factor in weed seedling recruitment models results in the accuracy of model being negligible as differences in the climate from year to year will result in differing weed communities, regardless of the complexity of the model (Auld and Coote, 1990).

Unfortunately, our understanding of the ecology behind weed seedling recruitment and the mechanisms underlying the spatial variability of weeds has fallen behind our capacity to treat the symptoms through technological advances in site-specific management (Rew and Cousens, 2001). By performing simple experiments determining both the seed and microsite limitations for weed seedling recruitment under a number of locations and habitats (Crawley, 1990), we will increase our understanding of the ecology of weed seedlings and decrease the gap between the technological advances and the mechanistic understanding of spatial weed variability (Rew and Cousens, 2001). The objective of this research project is to help bridge the gap between the basic biology of weeds and the technology used to control weed problems.

3. Effect of Tillage and Nitrogen Rate on Indigenous Weed Population over Three Landscape Positions

3.1 Introduction

Weed monitoring techniques indicate that weeds occur in distinct patches within a field (Palmer, 1992; Moloney and Levin, 1996; Gerhards et al., 1997; Clay et al., 1999; Dale, 1999; Dieleman et al., 2000). Observations indicate that the majority of these patches are located where soil moisture and nutrients are more favorable for weeds to germinate. These weed patches are typically limited to short distances within fields (Colbach et al., 2000b). Although this distribution of weed patches within agricultural fields and the congregation of species within these patches have been well articulated by survey techniques within the literature, there is a limited mechanistic understanding of why weeds species aggregate within a field (Dieleman et al., 2000). A greater understanding of the mechanisms would allow for a better understanding of the biology of weeds within agricultural fields.

Much research has been initiated determining the germination and establishment of weeds within relatively uniform landscapes. Within these uniform agricultural landscapes, where slope of the land has minimal influence on weed seedling recruitment, management practices that disturb the soil through tillage have had contrasting results, illustrating increased seedling recruitment (Peters, 1991; Mulugeta and Stoltenberg, 1997; McGriffin et al., 1997), equivalent recruitment to no tillage operations (Derksen et al., 1994), or decreased recruitment in comparison to no tillage (Spandl et al., 1997; Anderson et al., 1997). The addition of nitrogen fertilizer to a crop has also resulted in

conflicting results, with the addition of nitrogen resulting in increased germination (Williams and Harper, 1965; Agenbag and Villiers, 1989; Kirkland and Beckie, 1998), no difference in weed germination (Jornsgard et al., 1996), as well as decreases in total seedling recruitment with nitrate addition up to 448 kg N ha^{-1} (Fawcett and Slife, 1978). For the specific species that inhabit a landscape, the potential seed and microsite requirements may prevent or promote germination and establishment. A better understanding of the variability of the weed species within a landscape as well as the microsite requirements of these species will help in determining why and potentially where weed species will exist within a field.

Successful seedling recruitment, or the establishment of a small seedling via germination and emergence, is the essential first step in annual weed population dynamics (Harper, 1977) and under ideal conditions the most critical step in the establishment of a species. However, under contrasting landscape positions it is not known if seedling recruitment is the most important factor determining the spatial distribution of weeds. There is considerable variability observed in the seedling recruitment of individuals under uniform environments. Therefore one objective of this study is to examine and determine some of the factors resulting in the annual weed seedling recruitment of an indigenous weed population in three contrasting landscape positions. This study should lead to a greater understanding of the role that seedling recruitment plays in the establishment of a species within contrasting landscape positions and determine which species will recruit along the differing landscape positions. In addition, the objective was to determine if management practices, particularly tillage system and nitrogen application, have an influence on annual weed seedling recruitment.

3.2 Materials and Methods

A split-plot design was utilized for this experiment with landscape position as the main plot and management practice as subplots with five replicates at each landscape position. This experiment was conducted on a zero-tillage hummocky glacial till field near St. Denis, Saskatchewan during the summers of 2001 and 2002. Prior to initiation of this experiment, the land was farmed uniformly as a single field under minimum tillage cropping practices for several years with wheat as the previous crop in 2000. Weed populations present at the initiation of the study indicated the indigenous weed population of the field.

Segregation of the topographically defined landform segments was accomplished utilizing both topographical survey techniques and the use of a Digital Elevation Model (DEM) (Pennock et al., 1994). Each 10m by 10m cell of the DEM was classified into five landform position classes (convex upper slopes, linear mid slopes, concave lower slopes, high catchment levels, and low catchment levels). Five replications were positioned in varying points within a 10-acre section of land within the three main landform complexes (convex upper slopes, linear mid slopes, and concave lower slope positions). The convex upper slope positions were categorized as Orthic Regosols or Calcareous Chernozems; 30% sand, 43% silt, 27% clay; 1.8% organic C. The linear mid slope positions were categorized as Orthic Chernozems; 34% sand, 41% silt, and 25% clay; 2.2% organic carbon. The concave lower slope positions were categorized as Eluviated Chernozems or Luvic Gleysols; 24% sand, 46% silt, and 30% clay; 3.2% organic C. The treatments were completely randomized within each landform complex.

This trial consisted of five treatments within each landscape position, which were the main plots for the analysis. Within each landform element complex the management

practices treatments included an unfertilized control in conventional till treatment, 1X treatment of nitrogen which consisted of a pre-seed broadcast application of nitrogen in the form of urea fertilizer (46-0-0) at 75kg actual N ha^{-1} in both conventional (chisel plough) and zero tillage systems based on soil survey recommendations, as well as a 2X rate of nitrogen (150 kg actual N ha^{-1}) in both tillage systems. Upon completion of the broadcast application of nitrogen, tillage treatments were performed with a chisel plough in the same direction as the seeding. These tillage treatments were conducted one to two days prior to seeding.

Following seeding of the plots, all annual weeds were counted within two 0.25m^2 quadrants to assess weed seedling recruitment. There were very few perennial weed species present in the survey and in the few cases where perennial species was present the quadrant was repositioned to exclude perennial species from the weed counts. Perennials were not included in the survey as there is some indication that the presence of perennials affects the seedling recruitment of annual plants (Rees and Long, 1992). The two sub-samples were averaged to obtain an individual species and total weed species composition for each treatment.

The trial was seeded using a cone seeder with disc openers (1.83 m in width with 23-cm row spacing) with wheat seeded in the first growing season and barley in 2002. After seeding, weed seedling recruitment counts began 20d after planting when the crop was in the 2-leaf stage (Zadok stage 12). Experimental procedures were conducted slightly differently in 2001 and 2002 due to complications with the first seeding procedure. In 2001, seedling recruitment counts were conducted each week for a period of three weeks to assess weed seedling recruitment. Following this, glyphosate was applied to the trial to kill all plants and wheat was reseeded with minimal disturbance.

Weeds emerging prior to the glyphosate application were considered cumulative pre-herbicide application weed seedling recruitment while weeds emerging after the glyphosate application were considered post-herbicide application weed seedling recruitment. Following the application of glyphosate only newly emerging weed species were counted beginning two weeks after the glyphosate application. This was determined by monitoring the weed growth stage. In 2002, counts were conducted for three weeks after emergence and then for three weeks after an in-crop spray application of a selective low residual herbicide, 2,4-D. Highest recruitment counts for both pre- and post-herbicide application were utilized for analysis of total weeds recruiting. Counts were stopped following herbicide application once no new recruits were seen in the weekly counts. Only plants recruiting after the spray application were counted in the post-herbicide application seedling recruitment survey determined by their growth stage.

In 2001, weather stations were erected along all three landscape positions and soil temperature was monitored at a depth of 10 cm. Due to minimal environmental differences between slope positions, only the midslope landscape position was monitored in 2002. Thus, only temperatures on the midslope positions were utilized for both years to remain consistent between years. Precipitation also was monitored.

Due to heterogeneous variance between years as well as differences in experimental procedures between years, each year was analyzed separately. Data were analyzed for analysis of variance using the GLM procedure of SAS (SAS Institute, 1998). General F-tests were used to determine the significant effects each of the treatments had on individual species and total weed seedling recruitment. Although all species in the survey were included in the analysis, only those species that were prevalent in all blocks were analyzed individually. Those species, including stinkweed

(*Thlaspi arvense)*, wild mustard (*Sinapis arvensis)*, wild buckwheat (*Polygonum convolvulus)*, and red rooted pigweed (*Amaranthus retroflexus*) that occurred sporadically were included in the overall weed population, but not analyzed individually. Mean comparisons were conducted using Fisher's Protected LSD with a significance level of 0.05. Tillage system and N rate were compared by conducting orthogonal contrasts between plots with 1X nitrogen and 2X nitrogen under both tillage systems. The 0N nitrogen treatments were not included in the contrasts as it was only performed for a conventional tillage system.

3.3 Results and Discussion

Analysis of variance indicated that landscape position had a significant effect on weed seedling recruitment in both growing seasons, with management practice resulting in a significant effect on cumulative weed seedling recruitment in both years, green foxtail in 2001 and Russian thistle in 2002 at a confidence level of 95% (Table 3.1 and 3.2). Overall, management practices had minimal influence on weed seedling recruitment, but others have suggested that management practices may result in specific weeds successfully recruiting and potentially changing the weed flora overtime as observed by Derksen et al. (1994). Variability within the replications within the treatments indicated that the weed population was variable across the experimental area with greater variability within cleavers, Russian thistle, and kochia between replications than wild oat and green foxtail. Wild oat and green foxtail would have resulted in the least variability within the replications on weed seedling recruitment.

Table 3.1: ANOVA of the seedling recruitment of indigenous weed species from three landscape positions (lower, mid, and upper slopes) and five different management practices (conventional tillage with 0kg N ha^{-1}, 75 kg N ha^{-1}, 150 kg N ha^{-1}, and zero-tillage with 75kg N ha^{-1}, and 150kg N ha^{-1}) on a hummocky glacial till field near St. Denis, SK in 2001.

	Volunteer canola		Cleavers		Wild oat		Green foxtail		Russian Thistle		Kochia		Total weeds	
Analysis	F value	P value	F value	P value	F value	P value	F value	P value	F value	P value	F value	P value	F value	P value
	---------- Pre Herbicide Application ----------													
Rep	1.63	0.18	4.20	0.00	1.13	0.35	2.28	0.07	4.20	0.00	5.05	0.00	2.86	0.03
LP**	1.58	0.21	8.86	0.00	10.98	0.00	0.46	0.64	6.39	0.00	3.57	0.03	12.51	0.00
System	2.17	0.08	1.95	0.12	2.29	0.07	3.47	0.01	1.00	0.41	0.46	0.77	6.46	0.00
LP*System	0.86	0.56	0.50	0.85	0.46	0.88	0.92	0.50	0.89	0.53	0.81	0.60	0.70	0.69
	---------- Post Herbicide Application ----------													
Rep	3.22	0.02	5.25	0.00	0.39	0.82	0.54	0.71	2.58	0.05	5.01	0.00	2.40	0.06
LP	0.65	0.53	7.29	0.00	0.87	0.43	7.10	0.00	34.41	0.00	11.22	0.00	13.77	0.00
System	1.60	0.19	0.36	0.83	0.59	0.67	1.40	0.25	0.61	0.65	0.49	0.75	0.17	0.95
LP*System	1.52	0.17	0.80	0.60	0.74	0.66	0.70	0.69	0.72	0.67	0.44	0.89	0.46	0.88
	---------- Combined Pre and Post Herbicide Application ----------													
Rep	2.05	0.10	4.71	0.00	1.11	0.36	0.41	0.80	3.72	0.01	5.89	0.00	2.99	0.03
LP	1.54	0.22	9.36	0.00	10.88	0.00	2.83	0.07	27.58	0.00	8.02	0.00	4.53	0.02
System	2.27	0.07	1.81	0.14	2.37	0.06	0.55	0.70	0.70	0.59	0.54	0.71	4.68	0.00
LP*System	0.93	0.50	0.37	0.93	0.50	0.85	0.99	0.45	0.52	0.83	0.66	0.73	0.75	0.65

**LP – Landscape Position

Table 3.2: ANOVA of the seedling recruitment of indigenous weed species from three landscape positions (lower, mid, and upper slopes) and five different management practices (conventional Till with 0kg N ha^{-1}, 75 kg N ha^{-1}, 150 kg N ha^{-1}, and zero-tillage with 75kg N ha^{-1}, and 150kg N ha^{-1}) on a hummocky glacial till field near St. Denis, SK in 2002.

	Wild oat		Green foxtail		Russian Thistle		Kochia		Total weed	
Analysis	F value	P value	F value	P value	F value	P value	F value	P value	F value	P value
	---------- Pre Herbicide Application ----------									
Rep	3.48	0.01	2.45	0.06	3.28	0.02	2.86	0.03	5.02	0.00
LP**	3.36	0.04	2.06	0.14	2.64	0.08	4.86	0.01	6.85	0.00
System	.074	0.57	1.81	0.14	5.02	0.00	0.89	0.48	2.50	0.05
LP*System	.032	0.95	0.45	0.88	0.35	0.94	0.84	0.57	0.61	0.77
	---------- Post Herbicide Application ----------									
Rep	3.46	0.01	3.63	0.01	0.66	0.62	3.55	0.01	1.52	0.21
LP	8.34	0.00	6.92	0.00	13.39	0.00	6.96	0.00	17.02	0.00
System	2.67	0.04	1.34	0.27	0.81	0.52	2.16	0.09	3.40	0.01
LP*System	0.56	0.81	0.30	0.96	0.32	0.95	0.47	0.97	0.30	0.96
	---------- Combined Pre and Post Herbicide Application ----------									
Rep	3.16	0.02	3.65	0.01	2.17	0.08	3.44	0.01	3.87	0.01
LP	8.17	0.00	6.94	0.00	6.75	0.00	6.34	0.00	12.60	0.00
System	2.22	0.08	1.33	0.27	3.68	0.01	1.39	0.25	2.77	0.04
LP*System	0.47	0.87	0.30	0.96	0.35	0.94	0.71	0.68	0.41	0.91

**LP – Landscape Position

3.3.1 Landscape Position Effects

3.3.1.1 Wild oat (*Avena fatua* L.)

Wild oat (*Avena fatua* L.) was present in both years of the survey with the majority of the seedling recruitment in 2001 occurring prior to herbicide application (Table 3.3). Higher seedling recruitment was observed in the lower slope positions with an average of 36 plants m^{-2} recruiting from the lower slope and 16 to 9 plants m^{-2} recruiting from the mid and upper slope in the combined recruitment counts, respectively. Typically under ideal moisture conditions in Manitoba, wild oat occurs more frequently in lower landscape positions (Manning et al., 2001). In 2002, there was a similar trend in the combined recruitment results with 59% of the total wild oat plants recruiting in the lower slope and 27 and 14% recruiting from mid and upper slopes, respectively (Table 3.4). The main difference between the two years was that in 2001 the majority of the wild oat plants germinated and emerged prior to the application of herbicide, whereas the opposite occurred in 2002 (Tables 3.3 and 3.4). Higher post-spraying seedling recruitment could be due to low soil moisture in the early spring followed by significant precipitation events occurring from mid June to the end of the growing season (Figure 3.1). Wild oat tends to recruit preferentially in areas of cooler climates and moist soil conditions (Sharma and Vanden Born, 1978). This late season rainfall may have initiated seedling recruitment for those seeds that did not have sufficient moisture earlier in the growing season, indicating perhaps a resource limitation rather than microsite limitation. The majority of seedling recruitment occurs close to the soil surface (Du Croix Sissons et al., 2000) and would recruit once moisture was available and the seed was in a non-dormant stage. Alternatively, some late emerging seedlings in 2002 may have germinated deep within the soil where moisture

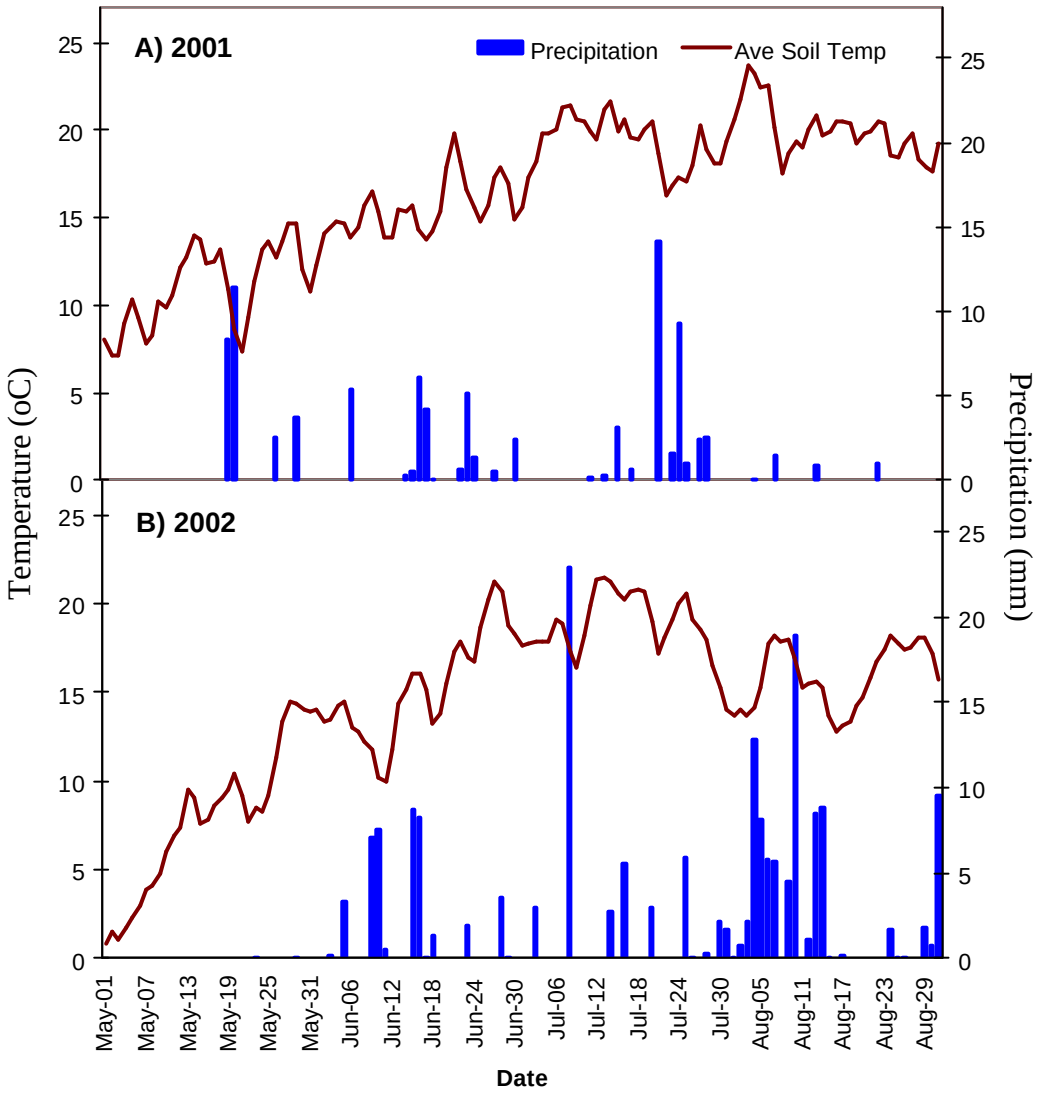

Figure 3.1: Precipitation and average soil temperature measurements at 10 cm for the midslope landscape position at St. Denis, SK in 2001 and 2002.

was not limiting, delaying the recruitment event as wild oat plants have emerged from depths up to 20 cm (Sharma and Vanden Born, 1978).

Table 3.3: The effect of landscape position on seedling recruitment of an indigenous annual weed population on a hummocky glacial till landscape near St. Denis, SK in 2001. Means consist of five differing management practices (conventional till with 0kg N ha^{-1}, 75 kg N ha^{-1}, 150 kg N ha^{-1}, and zero-tillage with 75kg N ha^{-1}, and 150kg N ha^{-1}).

	Seedling recruitment (Weeds m^{-2})			
	Landscape Position			
Weed Species	Lower	Mid	Upper	LSD*
Pre Herbicide Application				
Cleavers	95.6a	33.2b	22.4b	37.6
Wild Oat	33.2a	13.2b	7.2b	11.6
Green Foxtail	17.6	13.6	13.2	ns
Russian Thistle	4.0	1.2	0.8	ns
Kochia	1.2b	4.0ab	11.2a	7.6
Total Weed	164.0a	88.4b	63.2b	42.0
Post Herbicide Application				
Cleavers	13.2a	10.4a	5.2b	4.4
Wild Oat	2.8	2.4	2.0	ns
Green Foxtail	6.4b	19.6ab	31.6a	13.2
Russian Thistle	1.6b	3.2b	15.2a	3.6
Kochia	1.2b	1.6b	16.4a	7.2
Total Weed	30.8b	41.6b	72.8a	16.4
Combined Recruitment				
Cleavers	108.8a	43.6b	27.6b	40.0
Wild Oat	36.0a	15.6b	8.8b	12.0
Green Foxtail	23.6b	32.8ab	45.2a	18.0
Russian Thistle	5.6b	4.4b	19.2a	4.8
Kochia	2.4b	5.6b	27.6a	13.6
Total Weed	194.8a	132.0b	136.4b	46.8

*LSD (0.05) is for the corresponding row.
a-c Means followed by the same letter within each row are not significantly different according to the Fisher's Protected LSD (0.05).

Table 3.4: The effect of landscape position on seedling recruitment of an indigenous annual weed population on a hummocky glacial till landscape near St. Denis, SK in 2002. Means consist of five differing management practices (conventional till with 0kg N ha^{-1}, 75 kg N ha^{-1}, 150 kg N ha^{-1}, and zero-tillage with 75kg N ha^{-1}, and 150kg N ha^{-1}).

	Seedling recruitment (Weeds m^{-2})			
	Landscape Position			
Weed Species	Lower	Mid	Upper	LSD*
Pre Herbicide Application				
Wild Oat	3.6a	0.8b	0.0b	2.8
Green Foxtail	0.4	0.0	0.0	ns
Russian Thistle	70.8b	118.8ab	152.4a	71.6
Kochia	16.0b	20.4b	139.2a	89.6
Total Weed	96.0b	142.4b	292.0a	110.8
Post Herbicide Application				
Wild Oat	14.0a	7.2b	4.0b	4.8
Green Foxtail	52.8b	123.2a	88.4ab	38.0
Russian Thistle	22.8c	80.4b	119.6a	37.6
Kochia	11.6b	28.4b	92.4a	46.0
Total Weed	100.8b	239.2a	304.0a	71.2
Combined Recruitment				
Wild Oat	17.2a	8.0b	4.0b	6.8
Green Foxtail	52.8b	123.6a	88.4ab	38.0
Russian Thistle	93.6b	199.2a	272.0a	97.6
Kochia	27.6b	48.8b	231.6a	126.4
Total Weed	196.8c	381.6b	596.0a	159.6

*LSD (0.05) is for the corresponding row.
a-c Means followed by the same letter within each row are not significantly different according to the LSD (0.05).

3.3.1.2 Green Foxtail (*Setaria viridis* (L.) Beauv.)

Green Foxtail (*Setaria viridis (*L.) Beauv.) was present in both years of the survey (Tables 3.3 and 3.4). In 2001, there was no difference between the slope positions for pre-herbicide green foxtail seedling recruitment. After the application of herbicide, the highest seedling recruitment occurred on the upper slopes with an average

of 32 plants m^{-2} while the lower landscape position only had 6 plants m^{-2} successfully recruit. Overall, there was significantly higher seedling recruitment on the upper slope positions perhaps indicating xerophytic properties of green foxtail. Although green foxtail recruits preferentially under moister conditions, it has the ability to alter its root growth based on moisture conditions (Nadeau and Morrison, 1983). This characteristic may have allowed it to withstand harsher growing conditions to increase recruitment under arid upper slope positions. Increase in seminal root growth under low moisture conditions (Nadeau and Morrison, 1983) may allow this species to survive under drier conditions, indicating that the microsite for weed seedling recruitment is less important than its survival techniques as an established plant in under low soil moisture. The relatively high green foxtail recruitment from upper slopes may be more indicative of its ability to reproduce under adverse conditions, resulting in higher seedbank densities than expected in the upper slope positions. This enables green foxtail to remain western Canada's most prevalent weed over the past couple decades (Thomas and Wise, 1983; Leeson et al., 2003).

In 2002, there was almost no pre-spray seedling recruitment of green foxtail (Table 3.4). With June rainfall (Figure 3.1), there was significant post spray application seedling recruitment. There was relatively high seedling recruitment along all landscape positions with the highest nominal amount of seedling recruitment occurring along mid slopes at 123 plants m^{-2}, significantly greater than the 53 plants m^{-2} that recruited from the lower slope positions, while the upper slope positions had the middle seedling recruitment mean with 88 plants m^{-2}. One explanation could be that the mid slope positions would have sufficient resources for successful seedling recruitment with minimal light interception by the crop canopy, whereas in the lower landscape positions,

the high density of crop plants may have inhibited seedling recruitment due to a light limitation under the crop canopy (Reader and Buck, 1986) or the seedbank of the lower landscape positions had less green foxtail than the other slope positions. Along the upper slope positions, there may be adequate space, but lack of adequate water and nutrients may limit successful seedling recruitment. Typically, lower slope positions have higher organic matter in hummocky glacial till landscapes in northern Saskatchewan (Pennock and de Jong, 1990). Under low moisture conditions, the higher organic matter in the lower and mid slope positions may have allowed increased available water as soils with higher organic matter have higher water holding capacities.

3.3.1.3 Cleavers species (*Galium spp.)*

Cleavers (*G. aparine* L.) and/or false cleavers (*G. strumarium*)) was only present in the survey in 2001 (Table 3.3). There were many seedlings recruiting prior to herbicide application with minimal seedling recruitment occurring after the application of glyphosate. Seedling recruitment occurred early in the season when moisture was presumably non-limiting, which was as expected since cleavers thrive in temperate regions under moist conditions (Malik and Vanden Born, 1988). There was minimal seedling recruitment later in the growing season with the majority of late season recruits occurring in the lower landscape position. Although cleavers did germinate and emerge from all landscape positions, the majority of the plants occurred in the lower slope positions prior to herbicide application indicating a preference for seedling recruitment where adequate moisture was available.

3.3.1.4 Russian thistle (*Salsola pestifer* A. Nels.)

Overall in 2001, there was minimal seedling recruitment of Russian thistle (*Salsola pestifer* A. Nels.) with the most seedling recruitment occurring on the upper slope positions after the spray application (Table 3.3). The minimal late season moisture may have limited seedling recruitment of this C4 species with there being limited moisture during the critical time of emergence for Russian thistle to recruit.

In 2002, successful seedling recruitment of Russian thistle occurred both prior to and following herbicide application (Table 3.4). Although seedling recruitment was high within all landscape positions there was more seedling recruitment along the upper slope positions (152 plants m^{-2}) than the lower slope positions (71 plants m^{-2}) prior to in-crop herbicide application. Following adequate moisture requirements for seedling recruitment, Russian thistle tends to grow preferentially in dry sandy soils once established (Crompton and Bassett, 1985). Following herbicide application, seedling recruitment was again greater from the upper slope position (120 plants m^{-2}) than either the mid or lower landscape positions (80 and 23 plants m^{-2}), respectively. This relatively high late season germination is expected as Russian thistle has greater germination under high temperatures than C3 species (Crompton and Bassett, 1985). Overall, higher seedling recruitment along the upper and mid slope positions may indicate the microsite requirements for Russian thistle are met along the upper slope positions more than the lower slope positions. However, the seedbank dynamics of the slope positions was not analyzed and the upper and mid slope positions may have had higher Russian thistle population in the seedbank. Increased abundance of Russian thistle could also be accounted for by increased competitive ability under water stress due to root systems that can reach up to 1m in depth (Allen, 1982), thus increasing the

seed production in previous years, particularly after the crop died. Additionally, dry soil conditions especially on the upper slope positions decreased the ability to cultivate to similar depths between slope positions (personal observation). The shallower tillage on the upper slopes may have increased Russian thistle recruitment by keeping the weed seeds closer to the soil surface for rapid seedling emergence for both the tillage treatments and thus having higher levels of seedling recruitment. Previous research indicates tillage of weed seeds deeper than 6 cm decreases Russian thistle emergence (Crompton and Bassett, 1985) and in no-till systems, Russian thistle has had increased recruitment (Koskinen and McWhorter, 1986). Again, the crop canopy in the lower slope positions may have prevented late season recruitment from occurring to a greater extent than the upper or mid slope positions (Reader and Buck, 1986).

Russian thistle drought tolerance and tumbleweed dispersal mechanism within a field will allow it to spread easily within a field. This allows more uniform dispersal than other weed species allowing Russian thistle to persist along upper landscape positions where its microsite requirements are met and its competitiveness under arid conditions maintains a high population in the upper and mid slope positions.

3.3.1.5 Kochia (*Kochia scoparia* (L.) Schrad.)

As with Russian thistle, there was minimal seedling recruitment of kochia (*Kochia scoparia* (L.) Schrad.) in the 2001-growing season with the majority of seedling recruitment occurring following herbicide application along the upper slope positions (Table 3.3). Over the entire growing season, there was an average of 28 plants m^{-2} successfully recruit from the upper landscape position, significantly greater than the 2 and 6 plants m^{-2} in the lower and mid slope positions, respectively.

In 2002, kochia seedling recruitment was high both prior to and after herbicide applicatio n (Table 3.4). In both survey times, there was significantly higher seedling recruitment along the upper landscape positions in comparison to both the lower and mid slope positions. Kochia, a drought and salt tolerant plant (Douglas et al., 1985) had an average of 232 plants m^{-2} emerging within the upper slope, which was significantly greater than the 28 and 49 plants m^{-2} that occurred along the lower and mid slope positions respectively. Kochia has excellent tolerance to moisture stress with 45% of moisture stressed seeds still able to germinate at 13.2 bars of osmotic stress (Everts and Burnside, 1972). This may indicate that kochia is better adapted to decreased moisture conditions within the microsite for successful recruitment and subsequently its population persists under conditions experienced on the upper slope positions of the study.

3.3.1.6 Total Weed Community

The two growing seasons resulted in substantially different weed populations in terms of the species composition and the distribution of the species across the landscape (Table 3.3 and 3.4). In 2001, prior to herbicide application, cleavers and wild oat represented 79% of the total weed population in the lower slopes, 52% in the mid slope, and 47% of the upper slope positions (Table 3.3). With limited mid-season rainfall, minimal seedling recruitment occurred following the herbicide application with 50% of the total seedling recruitment following herbicide application occurring in the upper slope positions. Cumulative seedling recruitment numbers resulted in significantly greater weed seedling recruitment in the lower landscape position (195 plants m^{-2}) than mid (132 plants m^{-2}) and upper (136 plants m^{-2}) landscape positions. Preferential

moisture conditions early in the growing season (Fig. 3.1) may have filled the microsite requirements for cleavers and wild oat more than other species' studied in 2001, but there may have been more seeds in the soil profile as well.

In 2002, the highest seedling recruitment occurred in the upper landscape position followed by mid and lower landscapes with 55% of total recruitment in upper slopes pre herbicide application and 47% of total recruitment in the post herbicide application evaluation (Table 3.4). This may have been attributed to the residual effect of 2,4-D, which would have longer residual activity under low organic matter due to the ability of 2,4-D to bind to organic matter within the soil (Hermosin and Cornejo, 1991). The upper slope positions may have had reduced seedling recruitment post herbicide application in 2002 due to the lower organic matter in those soils. There was no cleavers seedling recruitment and only minimal wild oat seedling recruitment in 2002, which may have been a result of extremely low early season moisture along all landscape positions (Figure 3.1). These conditions resulted in the absence of microsite fulfillment for wild oat and cleavers during the early season window of seedling recruitment required for the C3 species.

Overall, Russian thistle, kochia, and green foxtail were the three main weed species present in the survey with the majority of the plants recruiting in the upper and mid-slope positions. Late season precipitation events (Figure 3.1) and the drought tolerance of these species allowed for fulfillment of the microsite requirements for successful weed seedling recruitment of the three C4 species with the additional rainfall during August and September allowing this species to survive after seedling recruitment. Ultimately, each landscape position was significantly different than the next with the highest seedling recruitment occurring in the upper landscape position (596 plants m^{-2}),

then mid slope (382 plants m^{-2}), and finally the lower landscape position (197 plants m^{-2}).

3.3.2 Effect of Nitrogen Rate

Overall, there was minimal influence of N rate on weed seedling recruitment in this experiment. Contrasts between 1X (75 kg N ha^{-1}) and 2X (150 kg N ha^{-1}) N rates indicated there was no effect of N rate on successful weed seedling recruitment for any weed species except green foxtail pre-herbicide application (Table 3.5). Contrasts between 0X and 1X N rates in conventional tillage indicated that no differences occurred in 2001 while Russian thistle had increased recruitment prior to herbicide application with N in 2002. In contrast kochia exhibited less seedling recruitment with 1X post herbicide application (Table 3.6). The effect of N on seedling recruitment has been inconsistent between studies with increased recruitment in some studies (Williams and Harper, 1965; Agenbag and Villiers, 1989; Kirkland and Beckie, 1998) and no effect in others (Jornsgard et al., 1996).

As there was no control plot for the 0X N rate for zero-tillage, it was not included in the comparison of N effects on weed seedling recruitment. Although this study resulted in a limited effect of N in either year, it does not conclusively indicate that N does not contribute to increasing or decreasing the available microsites for the weed species observed in the indigenous weed population. Within the 1X and 2X N treatments, one cannot definitively say that N had no effect on seed and microsite recruitments, but rather the results indicate that normal fertilizer techniques adequately accommodate the microsite and seed requirements for all annual weed species observed in this study. Increases from the typical N rate may have little effect on seedling

recruitment but will determine population dynamics of the plant community by influencing the competition between weed species and the crop (Blackshaw et al., 2003). This potential contrast in competition between N rates may have an influence on seed production and seedbank dynamics. In this experiment, the indigenous weed population was examined and as a result, the past year's N applications may have allowed a single species to dominate the seedbank and the subsequent recruitment counts by default.

Table 3.5: The effect of nitrogen rate on seedling recruitment of individual weed species when tillage systems (conventional, and zero-till) and landscape positions are combined (lower, mid, and upper) on a hummocky glacial till field near St. Denis, SK in 2001 and 2002. Significance determined by use of orthogonal contrasts.

			Seedling recruitment (Weeds m^{-2})		
Survey Timing	Weed Species	Year	$1N^{+}$	$2N^{++}$	Significance[z]
Pre Herbicide Application	Volunteer Canola	2001	5.6	6.0	NS
	Cleavers		47.2	42.4	NS
	Wild oat		14.8	18.0	NS
	Green foxtail		14.0	12.4	NS
	Russian Thistle		2.0	2.0	NS
	Kochia		5.6	6.0	NS
Post Herbicide Application	Volunteer Canola	2001	1.6	1.6	NS
	Cleavers		9.2	9.6	NS
	Wild oat		2.4	2.4	NS
	Green foxtail		18.8	19.2	NS
	Russian Thistle		7.6	6.0	NS
	Kochia		6.4	6.8	NS
Combined Recruitment	Volunteer Canola	2001	7.2	7.6	NS
	Cleavers		56.4	52.0	NS
	Wild oat		17.2	20.4	NS
	Green foxtail		32.8	31.6	NS
	Russian Thistle		9.6	8.0	NS
	Kochia		12.0	12.8	NS
Pre Herbicide Application	Wild oat	2002	1.2	1.6	NS
	Green foxtail		0.0	0.4	*
	Russian Thistle		107.6	149.2	NS
	Kochia		43.2	50.0	NS
Post Herbicide Application	Wild oat	2002	6.8	8.0	NS
	Green foxtail		79.2	83.2	NS
	Russian Thistle		68.0	77.2	NS
	Kochia		31.2	32.0	NS
Combined Recruitment	Wild oat	2002	8.0	9.6	NS
	Green foxtail		79.2	83.6	NS
	Russian Thistle		175.6	226.4	NS
	Kochia		74.4	82.0	NS

[+]Fertilizer rate of 75 kg actual N ha^{-1} as urea (46-0-0) broadcast and incorporated.
[++]Fertilizer rate of 150 kg actual N ha^{-1} as urea (46-0-0) broadcast and incorporated.
[z]NS = non-significant, * p = 0.05 to 0.01, ** p = 0.01 to 0.001, *** p = <0.001.

Table 3.6: The effect of nitrogen on seedling recruitment of individual weed species in conventional tillage when landscape positions are combined (lower, mid, and upper) on a hummocky glacial till field near St. Denis, SK in 2001 and 2002. Significance determined by use of orthogonal contrasts.

			Seedling recruitment (Weeds m^{-2})		
Survey Timing	Weed Species	Year	0N	1N*	Significance[z]
Pre Herbicide Application	Volunteer Canola	2001	10.4	8.4	NS
	Cleavers		72.8	64.0	NS
	Wild oat		23.2	16.8	NS
	Green foxtail		21.6	22.0	NS
	Russian Thistle		2.0	2.8	NS
	Kochia		4.0	6.4	NS
Post Herbicide Application	Volunteer Canola	2001	3.2	2.0	NS
	Cleavers		10.4	8.4	NS
	Wild oat		2.4	2.0	NS
	Green foxtail		19.2	16.4	NS
	Russian Thistle		6	8.0	NS
	Kochia		4.8	5.6	NS
Combined Recruitment	Volunteer Canola	2001	13.6	10.4	NS
	Cleavers		83.2	72.4	NS
	Wild oat		25.6	18.8	NS
	Green foxtail		40.8	38.4	NS
	Russian Thistle		8.0	10.8	NS
	Kochia		8.8	12.0	NS
Pre Herbicide Application	Wild oat	2002	1.6	1.6	NS
	Green foxtail		0.0	0.0	NS
	Russian Thistle		56.8	160.4	*
	Kochia		106.4	18.8	NS
Post Herbicide Application	Wild oat	2002	12.4	8.8	NS
	Green foxtail		116.0	96.0	NS
	Russian Thistle		80.8	81.6	NS
	Kochia		94.4	22.0	*
Combined Recruitment	Wild oat	2002	14.0	10.4	NS
	Green foxtail		116.0	96.0	NS
	Russian Thistle		137.6	242.0	NS
	Kochia		200.8	40.8	*

*Fertilizer rate of 75 kg actual N ha^{-1} as urea (46-0-0) broadcast and incorporated.
[z]NS = non-significant, * p = 0.05 to 0.01, ** p = 0.01 to 0.001, *** p = <0.001.

3.3.3 Tillage Effect

Overall, conventional tillage had greater total weed seedling recruitment prior to herbicide application (Table 3.7). Weed populations in the different tillage treatments that were observed before herbicide application resulted in increased weed seedling recruitment for conventional tillage system over zero tillage system (Table 3.8). Greater seedling recruitment of all species in 2001 and Russian thistle in 2002 were observed prior to herbicide application with two to three times more recruitment in the conventional tillage systems (Table 3.7 and 3.8). Following herbicide application, tillage system had no influence on seedling recruitment except green foxtail in 2001 had higher seedling recruitment counts in zero-tillage (Table 3.8). The tillage application places the weed seeds that are in the seedbank in favourable microsites for successful seedling recruitment. This corresponds to studies that exhibit increased emergence under chisel plow in comparison to zero-tillage (Peters, 1991). Potentially, the tillage pass also increases the temperature of the soil as the solar energy of the sun heats the dark surface, which may increase early season seedling recruitment, particularly for C4 species. Although not documented in this study, the heat increase of the top 1cm of soil has been observed to increase by 4.5 to 8^0C depending on the previous crop residue layer (McCalla and Davey, 1946). The incorporation allows moisture to be accessible to the weed seed and provides the temperature requirements necessary to meet the microsite requirements of many weed species. The increase in seed-soil contact by tillage will have a beneficial effect on availability of moisture and nutrients to the emerging seedling.

Table 3.7: Orthogonal contrasts comparing conventional tillage versus zero-tillage of combined nitrogen treatments (1X and 2X) and landscape positions (lower, mid, and upper) on the total weed population on a hummocky glacial till field near St. Denis, SK in 2001 and 2002.

		Seedling recruitment (Weeds m^{-2})		
Survey Timing	Year	Conventional Tillage	Zero Tillage	Significance[z]
Pre Herbicide Application	2001	139.6	52.8	***
Post Herbicide Application	2001	45.6	51.6	NS
Combined Recruitment	2001	185.2	104.8	***
Pre Herbicide Application	2002	245.2	112.0	*
Post Herbicide Application	2002	224.0	161.2	NS
Combined Recruitment	2002	469.2	273.2	**

[z] NS – non-significant, * p = 0.05 to 0.01, ** p = 0.01 to 0.001, *** p = <0.001

Post herbicide application, there was no significant difference between tillage treatments, and only green foxtail, a non-competitive species when emerging after the crop (Douglas et al., 1985), had higher seedling recruitment in 2001 in zero-tillage but only at low frequencies. This occurs as the weed seeds are more affected by the availability of moisture for recruitment than the placement in a favourable microsite. The weed seeds that were placed in favourable microsites by the tillage pass would have already recruited before the spray application and subsequently would have no effect on future seedling recruitment. A tillage pass will effectively increase seedling recruitment depleting the weed seedbank with successful herbicide control (Peters, 1991). These early recruiting weed species will utilize resources and available water early in the growing season, valuable resources especially on arid upper slope positions.

Table 3.8: Orthogonal contrasts comparing conventional tillage versus zero-tillage of combined nitrogen treatments (1X and 2X) and landscape positions (lower, mid, and upper) on the individual weed species on a hummocky glacial till field near St. Denis, SK in 2001 and 2002.

			Seedling recruitment (Weeds m^{-2})		
Survey Timing	Weed Species	Year	Conventional Tillage	Zero Tillage	Significance[z]
Pre Herbicide Application	Volunteer Canola	2001	8.4	3.2	*
	Cleavers		64.8	24.8	*
	Wild oat		22.8	10.8	*
	Green foxtail		20.4	5.6	**
	Russian Thistle		2.8	1.2	*
	Kochia		7.6	3.6	NS
Post Herbicide Application	Volunteer Canola	2001	2.0	1.2	NS
	Cleavers		9.6	9.2	NS
	Wild oat		2.4	2.0	NS
	Green foxtail		13.2	25.6	*
	Russian Thistle		7.6	6.0	NS
	Kochia		6.0	5.6	NS
Combined Recruitment	Volunteer Canola	2001	10.0	4.4	*
	Cleavers		74.4	34.0	*
	Wild oat		25.2	12.8	*
	Green foxtail		33.6	33.6	NS
	Russian Thistle		10.4	7.2	NS
	Kochia		13.6	9.2	NS
Pre Herbicide Application	Wild oat	2002	2.4	0.4	NS
	Green foxtail		0.4	0.0	NS
	Russian Thistle		190.0	66.4	***
	Kochia		50.0	43.6	NS
Post Herbicide Application	Wild oat	2002	10.0	4.8	*
	Green foxtail		92.4	69.6	NS
	Russian Thistle		86.8	58.4	NS
	Kochia		34.4	28.4	NS
Combined Recruitment	Wild oat	2002	12.4	5.2	*
	Green foxtail		92.8	69.6	NS
	Russian Thistle		276.8	124.8	**
	Kochia		84.4	72.0	NS

[z]NS = non-significant, * p = 0.05 to 0.01, ** p = 0.01 to 0.001, *** p = <0.001. Significance determined by orthogonal contrasts.

Agronomically, from this experiment, producers could expect an increased weed population after conventional tillage, early in the growing season. In addition, the lower slope positions will have higher densities early in the growing season. This could decrease both the available nutrients and water for a successful crop stand, particularly in years where moisture is the main limiting factor to crop production. Zero-tillage not only decreased the potential available micosites early in the growing season for successful seedling recruitment, but would decrease the available nutrients and water that the weed flora uses prior to crop establishment. If seeding is delayed for any reason in the spring, a spring burn-off in either system may be sufficient to prevent yield loss due to later emerging weeds.

3.3.4 Habitat differentiation among weed species studied

Overall, there was a general trend towards three contrasting types of weed species in this experiment. Cleavers and wild oat are two weed species that had higher densities in lower slope positions where water and resources tend not to be limiting for successful weed seedling recruitment and growth. In contrast, kochia and Russian thistle tend to aggregate along the upper slope positions. They tend to occupy space with higher stress levels, and uncertain moisture conditions, thriving on minimal moisture and high heat conditions (Everts and Burnside, 1972; Crompton and Bassett, 1985). Green foxtail tends to be an intermediate of the two types of weed species with relatively high seedling recruitment across all landscape positions with greater overall seedling recruitment later in the growing season along the mid and upper slope positions. Green foxtail was the only weed species that was present in relatively high quantities in both years of the experiment (Tables 3.3 and 3.4). This suggests green

foxtail has the ability to recruit under contrasting moisture conditions as 2001 had early season moisture with minimal precipitation while 2002 had minimal early season moisture with late season precipitation events providing the bulk of the moisture for the growing season. For green foxtail, emergence is impeded at low soil temperatures (Blackshaw et al., 1981); however, peak emergence follows a significant precipitation event regardless of the timing of that precipitation (Douglas et al., 1985). The three C4 plants (green foxtail, Russian thistle, and kochia) that occurred naturally in the field tended to be found along the upper and mid slopes with the two C3 plants (wild oat and cleavers) preferring the cooler, moister lower landscape positions. This delineation of the C3 and C4 plants would not hold true for all weed species. Seedling recruitment of each species in this experiment is determined by the specific microsite requirements of the weed seed and the seedbank population of the weed flora that had been established over years of continuous agriculture. The seedbank dynamics at each particular slope position would be an indication of the yearly seedling recruitment and seed return through reproduction over time. Nonetheless, three different microsite requirements and their subsequent seedling recruitment are exhibited by the five main species observed in this study, representing potentially habitat differentiation of weed species prevalent in western Canadian agriculture. Future work could concentrate on determining whether this observation is consistent with all weed species that dominate arable agriculture by mechanistically testing if seedling recruitment varies consistently for various slope positions. As a result, one could better categorize each weed into their respective ecotypes.

3.4 General Conclusions

From the results indicated above, one can conclude that landscape position has a significant effect on the seedling recruitment of annual weed species. Cleavers and wild oat weed species preferentially occurred within the lower slope positions in an indigenous weed population, while Russian thistle and kochia occur primarily along the upper slope positions within a given landscape. Those species that have the ability to recruit relatively equally along all slope positions (i.e., green foxtail) tend to be the most prevalent weed species in weed surveys (Thomas and Wise, 1983; Leeson et al., 2003). It is important to determine the factors that determine successful seedling recruitment within variable landscapes. There are many underlying factors, such as organic matter, soil moisture content, soil texture, etc. that can be the main reason for successful seedling recruitment of a species in species landscape locations. To better understand the basic biology of weed species, one must determine the main contributing factor, either seed production, microsite limitation, dormancy, resource limitation for weed seedling recruitment along each landscape position.

Tillage system is also a determinant in annual weed seedling recruitment with zero-tillage systems ultimately decreasing overall weed seedling recruitment in comparison to chisel plough conventional tillage systems, particularly in early season seedling recruitment. Observations from this experiment suggested that it is important to determine if tillage system in a controlled experiment with a known weed seedbank will agronomically decrease the amount of annual weeds that successfully recruit.

From this experiment, the rate of nitrogen fertilizer normally applied to the soil pre-emergent of the crop by producers does not significantly affect the overall weed seedling recruitment. The 1X soil nitrogen rates were applied at 75 kg N ha^{-1} based on

soil test results conducted prior to the season. Nitrogen is applied annually in crops and the effect of no nitrogen applied versus a typical nitrogen application appears to be of little agronomic importance under modern agricultural practices. As a result, only research focusing on rates, types of nitrogen fertilizer, or application techniques should be pursued in determining their effect on successful annual weed seedling recruitment.

4. Effect of Landscape and Moisture Availability on Annual Weed Seedling Dynamics

4.1 Introduction

Despite observations indicating certain weeds have the ability to congregate within different areas within the landscape as documented in Chapter 3, the mechanistic understanding of whether these weeds are limited due to seed availability or microsite availability for weed seedling recruitment remains relatively unknown. Although observations indicate weeds occur in patches (Palmer, 1992; Moloney and Levin, 1996; Gerhards et al., 1997; Dale, 1999; Clay et al., 1999; Dieleman et al., 2000) these patches are limited to small areas within a given field (Colbach et al., 2000b). Surveys indicate that the majority of these weed patches are located where soil moisture and nutrients are favorable. An increase in moisture within the lower landscape typically is attributed to increased weed populations in the lower landscape positions, although empirical research techniques have never been applied to determine if moisture is the main limitation along the upper landscapes.

The differences in weed seedling recruitment along contrasting landscape positions may be because of differences in productivity. Topography influences the redistribution of soil particles, organic matter, and soil nutrients, resulting in characteristic changes in both the chemical and physical properties along slope positions (Pennock and de Jong, 1990). These topographical influences results in characteristic changes in the overall productivity of the landscape depending on the moisture during

the growing season (Kravenchenko and Bullock, 2000), but the influence on seedling recruitment numbers remains largely undefined in the literature.

In the previous chapter, it was observed that certain species, specifically Russian thistle and kochia, might be able to germinate at higher levels along upper slope positions as compared to other species. In contrast, it has been observed that some species, including wild oat tend to recruit in lower landscapes when moisture is less limiting (Manning et al., 2000). The ability of specific species to recruit preferentially in upper or lower slope positions could not be specifically determined because the initial seedbank population in the soil described in Chapter 3 was undetermined. It is not known if under equivalent seedbanks, the addition of water to a landscape with largely unfavourable microsite conditions would increase seedling recruitment to equivalent levels of that in a different part of the landscape with more favourable microsite conditions. Within agricultural landscapes, the erosional surfaces observed on shoulder slopes due to years of wind and tillage erosion tend to be less favourable for seedling recruitment than the more sheltered lower landscape positions. It is important to understand the biological significance of the microsite of different species to determine if microsite is the main factor in seedling recruitment and establishment of weeds in patches.

The objective of this experiment was to determine if microsite availability for weed seedling recruitment is inherently different along contrasting landscape positio ns for three different weed species. This experiment was designed to determine if different weed species have different microsite requirements and inherently recruit preferentially in specific landscape positions. In addition, the experiment will determine if water is the

main limiting factor for the differences in microsite availability and whether weed seedling recruitment is similar across landscapes when a moisture limitation is removed.

4.2 Materials and Methods

This experiment was conducted at one location during the summers of 2001 and 2002 on a hummocky glacial till field near St. Denis, Saskatchewan. A split-plot randomized complete block research design was implemented with landscape position as the main plot with weed species (wild oat (*Avena fatua* L. or AVEFA), green foxtail (*Setaria viridis* (L.) Beauv. Or SETVI), and wild mustard (*Sinapis arvensis* L. or SINAR)), and irrigation regime (non-irrigated and 25 mm irrigation week^{-1}) included in the sub-plot treatments. There were three replicates for each landscape position. Segregation of landscape position (concave lower slope positions, linear mid slope positions, and convex upper slope positions) was aided with the use of a Digital Elevation Model (Pennock et al., 1994) map as well as visual examination of the area. The convex upper slope positions were categorized as Orthic Regosols or Calcareous Chernozems; 30% sand, 43% silt, 27% clay; 1.8% organic C. The linear mid slope positions were categorized as Orthic Chernozems; 34% sand, 41% silt, and 25% clay; 2.2% organic carbon. The concave lower slope positions were categorized as Eluviated Chernozems or Luvic Gleysols; 24% sand, 46% silt, and 30% clay; 3.2% organic C.

Wild oat, green foxtail and wild mustard were utilized as the weed species due to the availability of viable seed and the contrasting growth characteristics of the three annual weed species. Seeds for all three species were collected from previously harvested patches of weeds located at Agriculture and Agri-Food Canada Scott Research Farm, Saskatchewan. Green foxtail and wild mustard were harvested in 1997 while wild

oat was harvested in 2000. Upon completion of seeding by the producer, weed seeds were spread evenly at a rate of 12,500 viable seeds m^{-2} over a micro-plot area 0.5 m by 0.5 m in size. Weed seeds were incorporated into the soil to a depth ranging from 0 cm to 2.5 cm using a garden rake. Crop planting and weed seed incorporation was conducted on May 18, 2001 and May 24, 2002, respectively.

A flood irrigation method was used for the experiment, which utilized a 0.5 m by 0.5 m open-ended box 75-mm in height constructed of Plexiglas to prevent water from running down slope and a garden watering can. Water was added to each irrigation treatment plot at a rate of 25 mm $week^{-1}$ for a total of eleven weeks beginning 3d after weed seeds were incorporated for both growing seasons. Weed seedling recruitment counts were conducted on the entire plot area for each treatment once per week until the completion of the experiment. Time Domain Reflectometry (TDR) measurements were performed periodically throughout the experiment to a depth of 15 cm on the green foxtail plots to determine the differences in soil moisture content at each landscape position and irrigation treatment (Jacobsen and Schjonning, 1993). The TDR equipment utilized was a Trase System I from the SoilMoisture Equipment Corporation and utilized a cable length of 1.1 m. Although TDR measurements were performed in both years, only 2001 data were analyzed as negative water percentage values and moisture content greater than 100% observed in 2002 decreased the confidence in the results, perhaps indicating equipment failure. In addition, soil temperature at 10 cm and precipitation were monitored throughout the course of the experiment by an on-site weather station located on a midslope position in the field.

For 2001, germinable indigenous weed population was determined by taking 15 soil cores 9.5cm in diameter to a depth of 15cm from each landscape position and each

replicate. These soil cores were spread evenly in potting trays and germinated in the greenhouse during the months of September to December. Trays were watered daily to ensure adequate water was available for seed germination and weed seedlings were recorded after 21d. Four germination cycles were conducted with the soil being stirred after each cycle. At the end of the third cycle, a 30-day cold stratification period at 3^{o}C was utilized to potentially break the dormancy of any remaining viable weed species. The soils were stirred and placed back into the greenhouse to complete the germination study (Cardina and Sparrow, 1996). In 2002, an irrigated and non-irrigated control plot was added to the experimental design to account for the indigenous weed population. Seedling recruitment numbers utilized in subsequent analysis were considered the difference between the seeded plots and the indigenous weed population observed to recruit in the control plots. Only green foxtail, wild oat, and wild mustard were counted in the control plots. Weed populations in the control plots remained extremely low for wild oat and wild mustard with less than 8 and 4 plants m^{-2}, respectively. Green foxtail had a slightly higher population, but the largest indigenous population count was 208 plants m^{-2}, much smaller than the 12,500 seeds planted m^{-2} in the experiment.

Seedling recruitment was defined as the germination and emergence of a weed seedling and the protrusion of the plant above the soil surface (Harper, 1977). When a known population of germinable seeds exists in the ground, a safe-site or microsite can be characterized by a successful seedling recruitment event (Harper et al., 1965). Seeding densities of 12,500 plants m^{-2} were utilized to potentially fill all microsites within the soil profile for seedling recruitment, thus eliminating seed limited recruitment. Cumulative seedling recruitment was determined by using the highest seedling recruitment counts in the analysis of variance, and plots were monitored weekly

to ensure maximum seedling recruitment counts were captured before density dependent mortality occurred. Non-invasive plant counts were performed to minimize disturbance to the soil, which could alter microsite dynamics within the soil profile.

The rate of seedling recruitment was determined by utilizing a modified germination index. Germination index is a weighted measure of the speed at which each species reaches maximum seedling recruitment and is calculated by:

$$GI = (1/T)[(7)(W1)+(6)(W2)+(5)(W3)+(4)(W4)+(3)(W5)+(2)(W6)+(1)(W7)] \quad [Eq. 1]$$

where: GI = Germination index, W*i* = the additional number of seedlings emerging during week *i*, and T = maximum number of seedlings recruited (Gealy et al., 1994). Weeks used in this experiment between years were based on Julien calendar days to ensure that differences between years were not an artifact of seeding date. This unitless equation was utilized to indicate the rate of seedling recruitment regardless of maximum seedling recruitment numbers for individual plots. The higher the number obtained by the germination index, the faster a weed species reached maximum seedling recruitment.

At the completion of the experiment, biomass measurements and seed counts were conducted by harvesting the entire plot area for each treatment. Biomass cuts were performed after seed formation prior to any weed seeds dispersing by natural dispersal mechanisms. Because maturity of the three species varied, biomass cuts were performed on a daily basis based on plant maturity. The biomass of green foxtail and wild mustard was harvested with the use of a belt thresher and hand sieved to obtain the weed seeds. Kernel weights were determined for wild mustard and green foxtail for each landscape position and water treatment by counting and weighing three sets of 250 seeds and

obtaining an average for the treatment. After sieving, the seeds were then weighed to obtain a total seed number. Wild oat seeds were counted individually.

To account for heterogeneous errors between years, data were transformed using a natural log transformation prior to analysis. The transformed data was then analyzed as a split-plot design for analysis of variance using the mixed procedure of SAS with landscape position as the main plot and irrigation and weed species as the sub-plots (Littell et al., 1996). General F-tests were used to determine the significance of treatment effects on seedling recruitment, germination index, biomass production, and seed production. Mean comparisons between treatments were determined using Fisher's Protected LSD with a significance level of 0.05.

4.3 Results and Discussion

4.3.1 Climatic and Moisture Conditions

Precipitation patterns were quite different between the two site years at St. Denis, Saskatchewan. Although both years in the study were relatively dry, 2001 had 75 mm less growing season precipitation than 2002 (Fig. 3.1). The main difference that could have affected seedling recruitment between 2001 and 2002 is the timing of the first precipitation event. Four precipitation events in May of 2001 allowed for more beneficial early season moisture conditions for weed seedling recruitment while in 2002, the first precipitation of 3.2 mm occurred June 14. June and July precipitation was greater in 2002 than 2001 after the June 14th precipitation event. These precipitation patterns could have an effect on the rate of seedling recruitment, the induction of germinable seeds into secondary dormancy (Baskin and Baskin, 1998), and the biomass and seed production that would occur in the non-irrigated plots.

Time Domain Reflectometry measurements on the green foxtail plots one hour following the irrigation procedure resulted in a significant water effect on soil moisture content (Table 4.1). As expected, the addition of water increased the soil moisture content. A lack of a water by slope position effect indicated each landscape position increased in moisture equally with the lower slope positions increasing from 12.5% in the non-irrigated plots to 25% in irrigated, midslope positions 9.7% to 25% and the upper slope positions 10.9 to 21%; each slope position increasing statistically equivalent. The moisture after irrigation did dissipated down to 15%, 13% and 13% for the lower, mid, and upper slope positions respectively, but the irrigated plots still had slightly higher water content than the non-irrigated 98h following irrigation (Table 4.1).

Table 4.1: ANOVA of Time Domain Reflectometry on July 17 and 20th, for one hour after irrigation application and 98 hours following irrigation in the green foxtail reference plot at three landscape positions (concave upper slope, mid slope, and convex lower slope positions) under irrigated (25 mm week^{-1}) and non-irrigated conditions on a field near St. Denis, SK in 2001.

Effect	F-value	P-value
	One hour after irrigation	
Rep (Slope position)		0.00
Slope position	1.77	0.41
Irrigation	107.95	0.00
Slope position*Irrigation	1.58	0.17
	98 hours after irrigation	
Rep (Slope position)		0.00
Slope position	0.85	0.64
Irrigation	4.33	0.06
Slope position*Irrigation	0.03	0.97

4.3.2 Cumulative Seedling Recruitment

Cumulative seedling recruitment was affected by slope position as well as the slope position by species and species by water interactions (Table 4.2). Large variation within treatments and years was observed in the raw data, decreasing the level of significance, particularly for the single effects of water and species with very few degrees of freedom. Relatively large F-values were generated for these effects (Table 4.2), but no significance was observed possibly due to low degrees of freedom in the analysis.

Table 4.2: ANOVA of cumulative weed seedling recruitment (log transformed data), and germination index (no./no.) for green foxtail, wild oat, and wild mustard at three landscape positions (concave upper slope, mid-slope, and convex lower slope positions) under irrigated (25-mm $week^{-1}$) and non-irrigated conditions on a field near St. Denis, SK in 2001 and 2002.

Effect	F-value	P-value
	Cumulative seedling recruitment	
Slope position	24.14	0.00
Species	4.66	0.16
Irrigation	9.04	0.16
Slope position*Species	2.16	0.08
Slope position*Irrigation	0.45	0.64
Species*Irrigation	9.08	0.00
Slope position*Species*Irrigation	0.48	0.75
	Germination index	
Slope position	0.63	0.61
Species	6.75	0.13
Irrigation	0.01	0.93
Slope position*Species	1.18	0.33
Slope position*Irrigation	0.34	0.77
Species*Irrigation	2.35	0.42
Slope position*Species*Irrigation	0.14	0.97

The significant species by irrigation treatment interaction indicated wild oat was the only species that had a statistical increase in cumulative seedling recruitment between the irrigated and non-irrigated treatments when all landscapes were combined (Figure 4.1). Each species had a nominal increase in seedling recruitment with irrigation, but the larger seeded wild oat was the only species that was significantly decreased. Nominally, green foxtail had the highest seedling recruitment under both irrigated and non-irrigated conditions, with back-transformed non-irrigated seedling recruitment being almost equivalent to wild mustard and wild oat under irrigated conditions (Figure 4.1). Percent seedling recruitment compared to the total viable weed seed densities seeded at the beginning of the experiment ranged from 19 to 32% for the irrigated treatments and 9 to 19% for non-irrigated treatments with green foxtail always the highest and wild oat the lowest seedling recruitment of the three species. The increased seedling recruitment from the non-irrigated to irrigated treatments indicates moisture was a limiting factor in weed seedling recruitment. However, without a slope position by irrigation effect on weed seedling recruitment (Table 4.2), moisture affects each slope position in the same manner, increasing weed seedling recruitment equivalently across all slope positions. This is most likely due to the drought conditions experienced during the experiment as low precipitation (Figure 3.1) and low over-winter snowfall, decreased the difference in soil moisture conditions across the slope positions in the non-irrigated plots although soil moisture was not determined prior to establishment of the experiment.

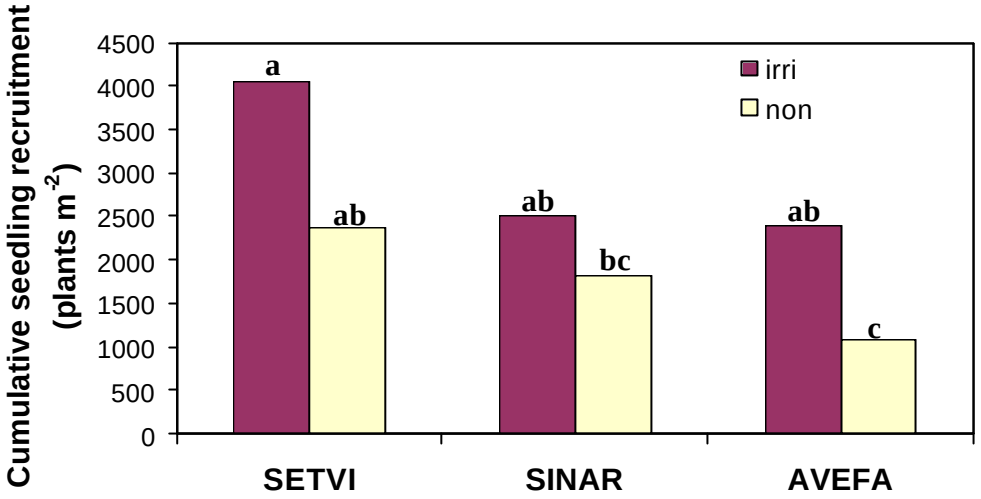

Figure 4.1: The effect of species by irrigation treatment on cumulative weed seedling recruitment (back-transformed data). Letters indicate LSD (p=0.05) based on the transformed data. SETVI, SINAR and AVEFA indicate green foxtail, wild mustard, and wild oat, respectively.

For each species, the lower and mid slope positions had greater seedling recruitment than the upper slope positions (Figure 4.2). The statistical method used in this experiment develops least significant differences for the interaction between and within species. Consequently, due to high variability within and between species, LSD within species was smaller than the LSD between species, which can result in smaller differences in wild oat being more significant than larger differences between wild oat and wild mustard (Figure 4.2). Green foxtail had higher seedling recruitment than wild mustard and wild oat in the upper slope position with nominal increases in the lower and mid slope positions (Figure 4.2). Between the three species, green foxtail seedling recruitment was the most similar across all slope positions with percent seedling recruitment ranging from 21 to 27% from upper to lower slope positions. Wild mustard and wild oat had lower seedling recruitment and slightly larger difference between the slopes with 13 to 22% and 9 to 17% percent recruitment, respectively. This trend of

stable seedling recruitment for green foxtail across landscape positions was also observed in the weed survey (Chapter 3). The innate ability of green foxtail to emerge and survive under the drier upper slope positions may be a determining factor why green foxtail remains the most prevalent weed species in western Canadian arable agriculture (Leeson et al., 2003).

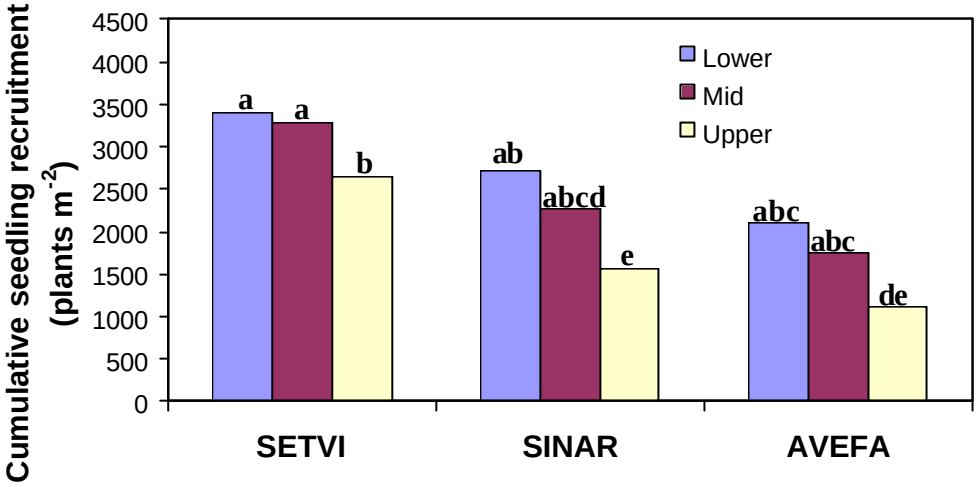

Figure 4.2: The effect of species by slope position on cumulative weed seedling recruitment (back-transformed data). Letters indicate LSD (p=0.05) based on the transformed data. SETVI, SINAR and AVEFA indicate green foxtail, wild mustard, and wild oat, respectively.

4.3.3 Germination Index (Rate of Seedling Recruitment)

Analysis of variance indicated there were no significant effects on the germination index of the species, measurement for the speed of seedling recruitment for the three species (Table 4.2). This indicates that the species germinated and emerged around the same time and reached maximum recruitment at about the same time regardless of the species, slope position, irrigation, or the interaction between the main effects. Seedling recruitment happened in a small time interval each year, regardless of

the environment, position along a landscape, or irrigation for the three annual species examined in this experiment. This suggests that a germinating seed reacts similarly whether it is in the upper slope or in the lower slope. This may be important for site-specific management as weed control can be performed in a single event without more weed seeds recruiting in specific landscape positions. Nevertheless, this experiment utilized an artificial seedbank seeded late in the spring where the effect of soil temperature on the rate of weed seedling recruitment was probably minimized as the soil temperature past May 20th was above minimum requirements for each species. Therefore, one might take some caution in relating the results to weed seedling recruitment from the natural seedbank.

4.3.4 Biomass and Cumulative Seed Production

Biomass and seed production means had similar differences but higher variability in seed production resulted in only a significant effect of slope position on the fecundity of the species (Table 4.3). Biomass production, being less variable, was significantly affected by slope position, irrigation, and species by slope position (Table 4.3). The significant effect of irrigation indicated the irrigation procedure increased average biomass from 73 to 170 g m^{-2} with combined species.

Table 4.3: ANOVA of cumulative biomass production (natural log transformed data) and weed seed production (natural log transformed data) for green foxtail, wild oat, and wild mustard at three landscape positions (concave upper slope, mid-slope, and convex lower slope positions) under irrigated (25-mm $week^{-1}$) and non-irrigated conditions on a field near St. Denis, SK in 2001 and 2002.

Effect	F-value	P-value
	Cumulative biomass production	
Slope position	17.76	0.00
Species	3.97	0.33
Irrigation	15.64	0.03
Slope position*Species	6.42	0.01
Slope position*Irrigation	0.66	0.54
Species*Irrigation	0.06	0.95
Slope position*Species*Irrigation	0.29	0.88
	Cumulative seed production	
Slope position	9.31	0.01
Species	1.04	0.46
Irrigation	18.43	0.14
Slope position*Species	1.93	0.23
Slope position*Irrigation	1.90	0.16
Species*Irrigation	3.10	0.37
Slope position*Species*Irrigation	2.06	0.10

The slope position by species interaction indicated that biomass production decreased from lower to upper slope, with no significant difference between slope positions for green foxtail (Table 4.3, Fig. 4.3). Biomass production of the three species indicated that green foxtail had no significant differences between landscapes, wild oat had significantly greater biomass production in the lower slope positions and there was a significant difference in biomass production for wild mustard at all three slope positions. In addition, wild mustard had lower biomass production than wild oat and green foxtail in the upper slope position and lower than wild oat in the mid slope position. Wild oat,

although having nominally the highest biomass production, resulted in the fewest weed seeds produced at all landscape positions. Green foxtail had uniform biomass production along all landscape positions (Figure 4.3), which indicated that seed production between the slope positions would be most similar across landscape positions for the species examined. In comparison, wild mustard and wild oat would result in dissimilar weed seedbanks from the upper to lower slope positions. This would influence future weed seed populations along the slope positions in an indigenous population. The amount of green foxtail seeds returned to the soil seedbank would be equivalent across all slope positions and consequently would increase in proportion along the upper slopes in comparison to the other two species.

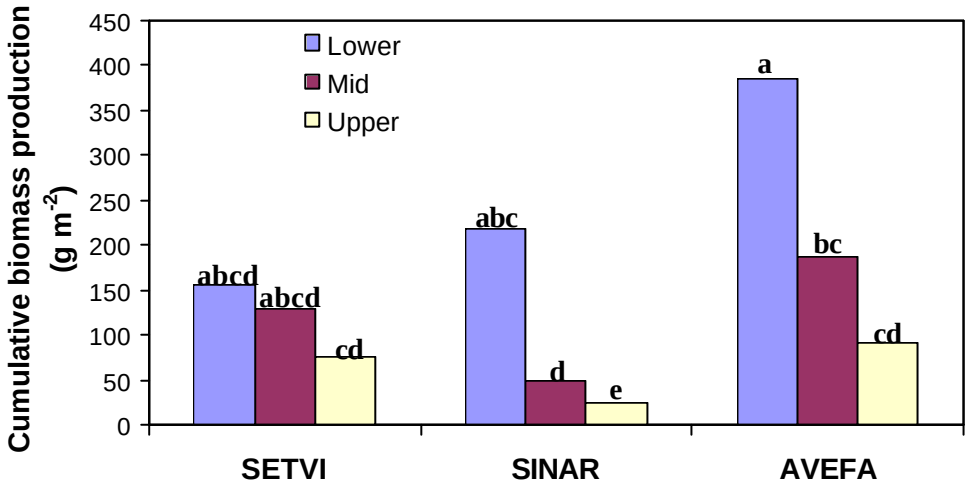

Figure 4.3: The effect of species by slope position on cumulative biomass production (back-transformed data). Letters indicate LSD (p=0.05) based on the transformed data. SETVI, SINAR and AVEFA indicate green foxtail, wild mustard, and wild oat, respectively.

4.4 Discussion

In this experiment, the goal was to eliminate potential seed limitation on weed seedling recruitment by over-populating the weed seedbank with 12,500 weed seeds m^{-2}

(Eriksson, 2000). As observed in another experiment, seed limitation was still prevalent in green foxtail and wild mustard up to 62,500 weeds m^{-2} (Chapter 5), by the effect of weed seedling recruitment was more based on microsite at the higher weed densities. Consequently, for the purposes of discussion, one can assume that there was minimal effect of seed limitation on the resulting weed population. Regardless of irrigation treatment, weed seedling recruitment never reached maximum seedling recruitment based on the target number of viable weed seeds incorporated, indicating that water was not the only limiting factor preventing weed seedling recruitment and does not eliminate microsite limited recruitment. Nonetheless, without the addition of water, less weed seeds recruited, indicating resources are limiting weed seedling recruitment, a form of microsite limitation. The lower and mid slope positions always had increased seedling recruitment in comparison to the upper slope positions for all three weed species selected, indicating that each species had higher levels of microsite limitation along the upper slope positions. The three potential fates of these weed seeds include predation or mortality prior to emergence, seeds remain non-dormant but lack a microsite for successful weed seedling recruitment, and seeds change dormancy state to secondary dormancy prior to seed germination (Radosevich et al., 1997). The conversion of weed seeds to secondary dormancy prior to seed germination would occur more often when germination was delayed due to poor moisture conditions or lack of necessary resources during the critical period for weed seedling recruitment (Radosevich et al., 1997).

Green foxtail appears to have the most uniform weed seedling recruitment of the three species across the three landscape positions. The ability of green foxtail to recruit along both contrasting moisture regimes (Fig. 4.1) and landscape positions (Fig. 4.2) suggests green foxtail recruits evenly under almost every environmental condition. The

ability of green foxtail to recruit evenly across all landscapes regardless of irrigation corresponds to the results observed in the weed survey (Chapter 3) where green foxtail seedling recruitment prior to herbicide application did not differ between upper and lower slope positions in either study year. Green foxtail also had limited reduction in weed biomass production across all slopes, which would limit the decrease in seed production along the upper slopes for the weed survey. Even under the drier conditions experienced in 2001 and 2002 there was no increase in seedling recruitment in green foxtail because of irrigation and biomass was also relatively unaffected, indicating a significant drought adaptation of this species.

Conversely, the highest seedling recruitment for wild mustard and wild oat was on the lower landscape positions corresponding to the survey results for wild oat where the greatest seedling recruitment occurred in the lower landscape positions (Chapter 3). Consequently, wild mustard and wild oat requirements for seedling recruitment are more fulfilled in the lower landscape positions. Nevertheless, the cause of the microsite limitation along the upper and mid slope positions is undetermined as topography influences the redistribution of particles, organic matter, and soil nutrients (Pennock and de Jong, 1990). This influence of topography will have a marked effect on factors such as soil fertility, moisture, soil temperature, soil textural properties, pH, or physical limitations to recruitment and can have a significant impact on seed germination dynamics.

Overall, wild oat had the lowest weed seedling recruitment perhaps indicating the larger seeded individual had different microsite requirements than the other two species. As well, seedling recruitment in wild oat had the greatest response to irrigation (Figure 4.1), indicating moisture is more important for successful seedling recruitment of this

large seeded species. Moisture is a limiting factor in weed seedling recruitment across all landscapes equivalently, but weed seedling recruitment was never increased by irrigation in the upper slope positions to a level equivalent to the lower slope positions. As the soil tests indicated, the upper slope positions could have been affected by the both the calcareous content of the soil and the reduced organic matter in comparison to the lower slope positions. Consequently, the upper landscapes had additional factors beside water that prevented weed seedling recruitment.

This experiment may not mimic a natural setting as weeds were incorporated mid-May in both years. Many factors could have influenced weed seedling recruitment if the experiment was initiated in early April prior to any germination. Temperatures in May were above base temperatures for any of the three species to germinate (Fernandez-Quintazilla et al., 1990; Cousens et al., 1992; Douglas et al., 1985), reducing temperature effects on seedling recruitment. In addition, the artificial seedbank was used to eliminate seed limitation as well as eliminate the dormancy effect of weeds in the seedbank as dormancy can decrease recruitment from a potential 60% recruitment for wild oat (Medd, 1996) to a low of 2.5% for wild mustard (Edwards, 1980) because of dormancy characteristics. Seeds were incorporated into the artificial seedbank to a depth where seedling recruitment would not be limited by depth (du Croix Sissons et al., 2000).

With hard rainfall, including the flood irrigation technique utilized, the upper slope positions had a visibly harder soil crust as compared to the mid and lower slope positions (Figure 4.5) likely due to increased Calcium carbonate levels. This could have physically prevented germinated seeds from emerging prior to death as some species can

not penetrate the crust that can form on soil (Stolzky and Barley, 1968), thus decreasing seedling recruitment along the upper landscape positions.

Moisture is a major factor limiting weed seedling recruitment, but it increased seedling recruitment in all landscape positions equivalently. It was anticipated that moisture would not be as limited in the lower landscapes and irrigation would result in only limited increases in seedling recruitment in the lower landscapes with larger increases in recruitment in the upper landscape positions. This lack of an irrigation by landscape effect indicates there are other overriding factors that ultimately limit weed seedling recruitment on the upper landscape positions besides moisture. The influence moisture has on weed seedling recruitment is only a partial reason why weeds recruit preferentially in lower landscape positions. As well, this study indicates that the absolute requirement of water for germination is met along each landscape position.

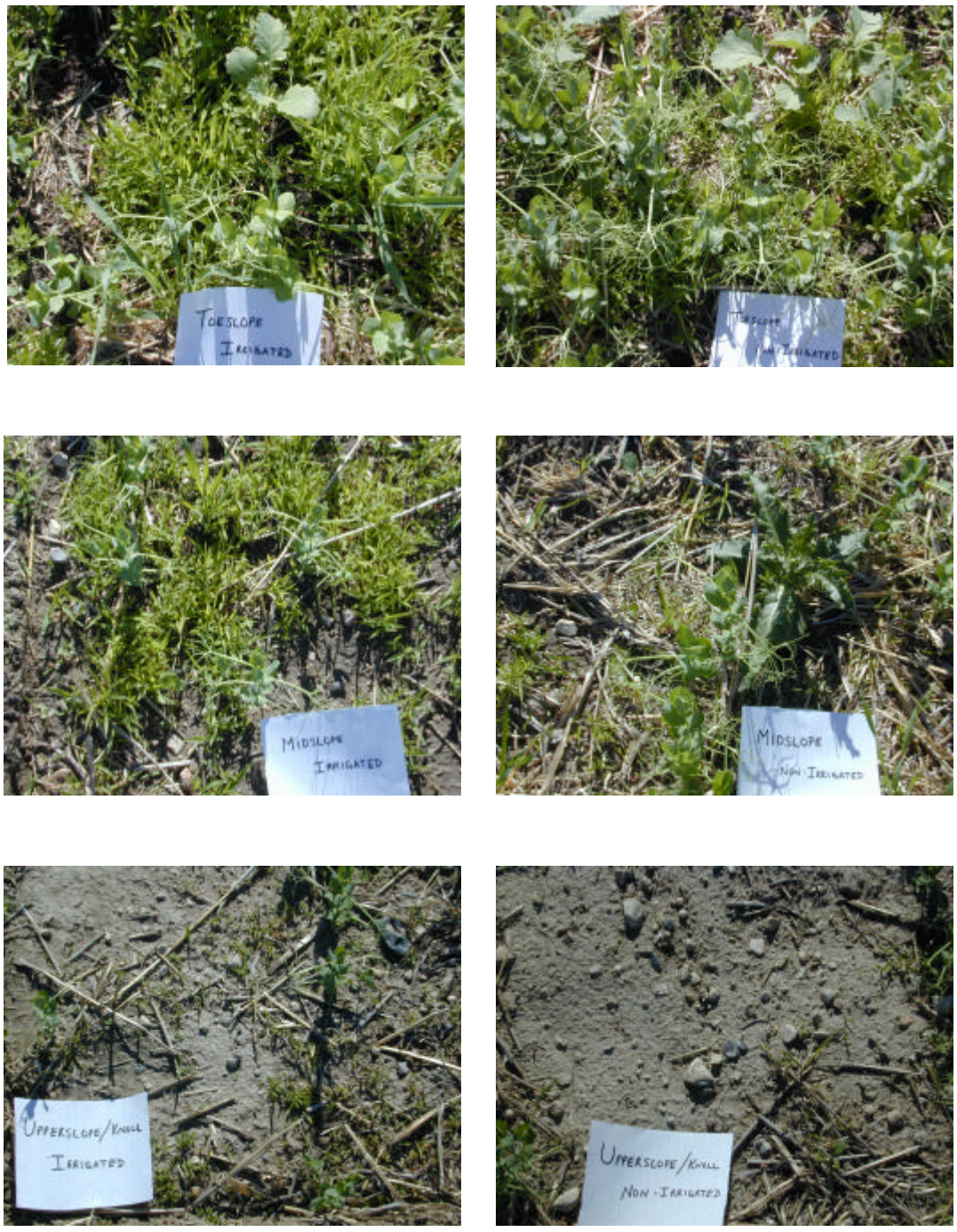

Figure 4.4: Weed seedling recruitment in 2001 along the three landscape positions with images on the right being irrigated while images on the left were non-irrigated. Lower landscape positions are located on the top, mid slopes in the middle and upper landscape positions at the bottom.

Agronomically, the decreases in weed seedling recruitment due to microsite limitation were minimal. It has been extensively examined that weed surveys indicate weed grow in patches (Palmer, 1992; Moloney and Levin, 1996; Gerhards et al., 1997; Dale, 1999; Clay et al., 1999; Dieleman et al., 2000: Colbach et al., 2000b). From this experiment it suggests that these patches are more a result of competition, growth and reproduction rather than differences in weed seedling recruitment. Microsite limitations were agronomically inconsequential as there were still many weed seedlings recruiting under non-irrigated upper slope positions. The irrigation treatment had a marked effect in seed production with only a significant increase in weed seedling recruitment for wild oat and not wild mustard or green foxtail. The accumulation of weeds in patches is most likely a result of increased reproduction resulting in increased seedbank numbers over time and it can be hypothesized that weeds such as green foxtail become more spatially homogeneous as seedling recruitment and seed production is relatively uniform across all landscape positions. Conversely, wild oat and wild mustard should develop in patches where moisture favours seed production as both these species will recruit at high levels along all landscape positions (Figure 4.2 and 4.3). There is a greater decrease in reproductive output in the upper and mid slope positions for these weed species, which results in decreases to the soil seedbank over time.

The addition of 25-mm of water per week for a period of eleven weeks did not increase recruitment in all species in a drought year indicated that there are other factors that limited overall seedling recruitment. The physical soil characteristics of the soil must be a major factor in determining safe site limitation of species with moisture being one of many factors that limit weed seedling recruitment. The removal of the main limiting factors in the germination process indicates that each species has a specific set

of conditions necessary for weed seedling recruitment. The weed seeds in this experiment were placed into the soil while non-dormant and were placed in a fertile seedbed relatively free of hazards with sufficient temperature for recruitment to occur; all essential aspects of the microsite concept (Harper, 1977). External factors such as soil texture, soil chemical properties, oxygen level within the microsite, optimal germination temperatures, and availability of specific resources not present in the study must have been more important microsite factors than originally expected. Resource limitation may ultimately be the most limiting factor in determining the total weed seeds that successfully recruit.

The relative importance of seed number on weed seedling recruitment could not be determined in this experiment as the same quantity of seed was used for each species. To better understand the influence of seed limited recruitment of weed seedling recruitment, a number of seeding densities should be utilized to delineate the seed limited recruitment effects from the microsite limited recruitment effects. The densities utilized in the experiment were to maximize the potential weed seedling recruitment from the seedbank and another experiment examining different seeding density on overall weed seedling recruitment would be necessary to better understand the differences between species on weed seedling recruitment. Consequently, future work could emphasize the species effect of contrasting densities of weed seeds for each species and water regime to better understand of the role seed limited recruitment had on weed seedling recruitment.

5. Effect of Tillage and Weed Density on Annual Weed Seedling Dynamics

5.1 Introduction

Although emergence of weed populations and plant densities within a field has been monitored extensively in western Canadian agriculture, there is limited research determining the main limiting factors in weed seedling recruitment. In ecological systems, Harper (1977) suggested that the microsites as well as the availability of seeds within a specific area may limit the successful seedling recruitment of many species, but the influence of microsites versus seeds within agricultural fields has largely been unexplored.

Within arable lands, agricultural practices have shifted to minimum and zero tillage systems across the western prairies. This shift in cultivation practices from conventional tillage to reduced tillage has been reported to result in both increased weed populations (Ball and Miller, 1993; McGriffin et al., 1997; Spandl et al., 1998), and decreased weed populations (Pickering and Raju, 1996; Anderson et al., 2002), as well as a change in species composition with no increases in weed populations (Swanton et al., 1993; Derksen et al., 1994). Utilizing survey techniques and observing the change over time as a system converts from conventional to reduced tillage systems have largely determined these changes in weed composition.

Within species, it has been observed that wild mustard (Anderson et al., 1998) and wild oat (Pickering and Raju, 1996) emerge at greater frequencies under conventional

tillage while green foxtail (Anderson et al., 1998) and other smaller seeded species (Kostinen and McWhorter, 1986) emerge at greater frequencies under zero tillage systems. It has been postulated that this increased recruitment by green foxtail is due to its ability to germinate from shallow depths (Buhler and Mester, 1991) but specific trials comparing species of different seed characteristics on the seedling recruitment remain limited. Although survey techniques have indicated shifts in weed populations under different tillage systems with preferential recruitment of certain species, no research has examined if seedling recruitment of these weeds were limited by seed number or the availability of microsites within the tillage system. A greater understanding of the main influence causing differences in weed seedling recruitment observed in previous studies may have determined the characteristic changes in weed populations that occurred over time.

Seedling recruitment of annual weed species is determined by both the availability of seeds within the soil, and the availability of microsites or safe-sites (Harper, 1977). Despite observations indicating that certain species persist under different tillage systems, the mechanism causing this change in species abundance under different tillage systems remains unknown. The objective of this experiment was to examine the influence of seed and microsite limitation on seedling recruitment of three different summer annual weeds under two different tillage systems. The importance of this experiment is to determine the applicability of the microsite limited recruitment versus seed limited recruitment on weed populations observed in arable agriculture in western Canada.

5.2 Materials and Methods

This experiment was conducted at two field locations during the summer of 2001 and 2002, the University of Saskatchewan Kernen Research Farm (lat 52°51' long 106°33') and Agriculture and Agri-Food Canada Scott Research Farm (lat 52.4° long 108.8°). Soils at the Kernen (Bradwell Dark Brown Chernozem; 26% sand, 34% silt, 40% clay; 2.9% organic C; pH = 6.7) were similar to those at Scott (Dark Brown Chernozem with 31% sand, 42% silt, 27% clay, 4% organic matter, and pH = 6.0), although Kernen had slightly higher clay content. A split-plot design with four replicates was utilized with tillage treatment being the main plot and varying densities of three annual weed species as the subplots.

Three annual weed species, wild oat (*Avena fatua* L. or AVEFA), green foxtail (*Setaria viridis* (L.) Beauv. or SETVI), and wild mustard (*Sinapis arvensis* L. or SINAR), were selected for this experiment based on their different growth characteristics and seed availability. Seeds for all three species were collected from previously harvested patches of weeds located at Agriculture and Agri-Food Canada Scott Research Farm, Saskatchewan. Both locations had been farmed in a minimum tillage system with wheat being the previous crop in 2000 at the Scott Research Station and chemical fallow was performed the previous year at the Kernen Research Station.

One-day prior to seeding the weeds, two tillage passes with a 20 cm wide sweep chisel plough were conducted on the tillage portion of the split plot. Each tillage pass was conducted across each rep to a depth of 10 cm in opposite directions to evenly incorporate the previous years' crop residue layer. Green foxtail and wild mustard seeds were broadcast using a modified peppershaker (Wilson and Wright, 1990), and wild oat

was broadcast by hand. The weed species were broadcast over a 1 m by 2 m rectangle located 1.5 m from the front edge and sides of each 4 m by 8 m plot. The target densities for green foxtail (*Setaria viridis* (L.) Beauv. or SETVI) and wild mustard (*Sinapis arvensis* L. or SINAR) were 20, 100, 500, 2,500, 12,500, and 62,500 viable seeds m^{-2}. Wild oat (*Avena fatua* L. or AVEFA) was not seeded at the 62,500 density due to the physical limitations in placing this many wild oat seeds m^{-2}. Seeds were tested for germination in the laboratory and seeding rates were adjusted accordingly to ensure the proper amount of viable weed seeds were applied to each treatment. Laboratory germination percentages for each species were as follows: green foxtail 80% and 92%, wild mustard 77% and 80%, and wild oat 78% and 80% in 2001 and 2002 respectively. The rear half of each plot was utilized as an individual control to account for the indigenous weed population.

After the seeds were broadcast, a 10 cm cultivation treatment was conducted on the tillage plots to incorporate the seeds. Plots were 4m in width to prevent any dispersal between treatments. Previous researchers had found that the method of cultivation used in this experiment disperses seeds a mean distance of 0.71 m with almost all seeds remaining in the surface 5 cm of the soil (Marshall and Brain, 1999). As a consequence, the 3 m buffer between the edges of each 1 m by 2 m rectangular treated area was sufficient to eliminate seed dispersal between treatments.

Following broadcasting of the seeds, wheat was seeded at 120 kg ha^{-1} and fertilized at a rate of 25 kg ha^{-1} actual of P_2O_5 and 70 kg ha^{-1} actual of N applied as urea, side-banded between the wheat rows. The seeding implement used at Kernen was a Fabro small plot seeder with disc openers (1.83 m in width with 23 cm row spacing),

while the seeding implement utilized at Scott had hoe drill openers (2.00 m in width with 28 cm row spacing). The seeding dates for Kernen and Scott were May 10 and May 14, 2001 and May 15 and 16, 2002, respectively.

Seedling recruitment is defined for this experiment as the germination and emergence of a weed seedling and protrusion of the plant above the soil surface (Harper, 1977). A microsite, defined as a small-scale site that immediately affects a seeds ability to germinate and emerge (Eriksson and Ehrlen, 1992), was characterized in this experiment by a successful seedling recruitment event. As the weed densities increased, the viable seeds seeded at the beginning of the experiment that remained non-emerged were considered to exhibit microsite-limited recruitment.

Seedling recruitment counts were conducted upon the observation of the first weed seedlings emerging followed by emergence counts every second week in 2001 and every week in 2002. Counts were conducted on each treatment both at the front and the rear of the 1 m by 2 m broadcast weed seeded area as well as two counts performed in the untreated section at the back of each 2 m by 8 m plot. Seedling recruitment numbers were calculated as the difference between the two treated areas and the average of the control plots at the rear of each plot. To account for the spatial variation in weed densities, particularly for green foxtail, which was the weed with the greatest indigenous population at either site, it was assumed that a species could not recruit greater than 100% or less than 0%. All plant counts that resulted in a negative number were indicated as zero recruitment and all plant counts that resulted in greater than 100% seedling recruitment were considered 100% recruitment. That is, when there should have been 20 plants m^{-2}, the maximum seedling recruitment could be 20 while the

minimum could be zero. The first weed counts in 2001 were conducted on June 4th at Kernen and June 7th at Scott, with final weed seedling recruitment counts conducted on July 18th and 20th, respectively. In 2002, initial weed seedling recruitment counts were performed on June 2nd in Kernen and June 4th in Scott, with final counts conducted on July 14th and 15th.

Germination index, a unitless variable, was calculated to determine the rate of seedling recruitment (Gealy et al., 1994). The formula used for germination index was:

$$GI = (1/T)[(5)(W1) + (4)(W2) + (3)(W3) + (2)(W4) + (1)(W5)] \quad \text{[Eq. 1]}$$

Where: GI = Germination index, Wi = the additional number of seedlings emerging during week i, and T = maximum number of seedlings recruited. Reductions in seedling recruitment counts due to mortality after maximal recruitment were considered zero recruitment and not negative values in the formula. This formula was utilized because it is density independent; comparing 12,500 plants m^{-2} with 20 plants m^{-2} densities does not affect the calculated rate of seedling recruitment. Germination index was only calculated for the 2002 data as the 2001 counts were not conduc ted weekly, which was not frequent enough to capture true emergence rates.

Biomass was collected at species-specific maturity, that is after seed formation but prior to weed seed dispersal by natural mechanisms. From this biomass, seeds were collected to determine the seed numbers produced. Harvest techniques included hand picking individual seeds off wild oat and counting harvested seeds to obtain seed numbers, while wild mustard and green foxtail were harvested with the use of a belt thresher with subsequent sieving to remove debris. Thousand-kernel weights for these

two species were obtained at each density and utilized to determine the seed number based on the mass of seeds obtained from the threshing and sieving process. Although data was obtained for biomass and seed production for all treatments and years, drought conditions inhibited the biomass and seed production for many of the species. The drought conditions observed in 2001 resulted in death of the plant before weed seed production for green foxtail in Scott and the second year of drought in 2002 resulted in death of all weeds before seed production. Death was extremely rapid, and plant biomass was not obtained for Scott in 2002. At Kernen, late season rainfall in 2002 resulted in seed production for green foxtail only. As a consequence of these arid conditions, the biomass data from 2001 only was analyzed.

Analysis was conducted on the percent emergence based on the target seedling densities and was performed on the highest seedling recruitment counts measured. Germination index was analyzed to determine the rate at which the weed species reached maximal seedling recruitment. To accommodate the assumptions of ANOVA and have normally distributed data within years, the percentage data were square root transformed before analysis (Littel et al. 1996). Neither field locations nor years had homogeneous variances based on Bartlett's test (Gomez and Gomez, 1984) when data was combined and subsequently each year and location was analyzed separately. The mixed procedure of SAS was utilized for the split-plot design of this experiment with tillage being the main treatment (Littell et al., 1996). General F-tests were used to determine the significant treatment effects for cumulative seedling recruitment, germination index, and biomass production. Mean comparisons were conducted using Fisher's Protected LSD with a significance of 0.05.

Regression analysis was performed using the regression procedure of SAS to determine the relationship between the percent seedling recruitment and the natural log of the density (SAS Institute, 1998). For each replication, a slope and an intercept were determined for each species. T-tests were performed for the slope and the intercept for species that exhibited linear effects to determine differences.

5.3 Results and Discussion

5.3.1 Weather Conditions

Both Kernen and Scott experienced drought conditions in 2001 and early in the season for 2002 (Fig. 5.1 and 5.2). Kernen had 127 mm and 216 mm of growing season precipitation in 2001 and 2002, respectively, which was below the 209 mm 30-year average (SAFRR, 2004) for 2001 and only late season precipitation in 2002 resulted in Kernen reaching the average growing season precipitation for Saskatoon, SK. Scott has had only one precipitation event during the 2001 and 2002 growing seasons over 25 mm (Figure 5.1). Scott experienced extreme drought conditions in both season with 128 mm and 144 mm of growing season precipitation, which is less than the 30-year average for North Battleford, the closest major center to Scott, of 225 mm of growing season precipitation (SAFRR, 2004). Kernen had less extreme drought conditions, but experienced two early season growing conditions with below average precipitation with the first substantial precipitation event occurring on June 11 in 2002. At Kernen, 2001 was characterized by an earlier season precipitation event (May 19th) with extremely low growing season precipitation while in 2002 severe drought conditions existing from the low precipitation in 2001 and the first substantial precipitation event occurring June 11th

followed by adequate late season precipitation (Figure 5.2). With the drought conditions experienced over the course of the study, the applicability of the microsite concept can be examined extensively in relation to arable agriculture. A moisture limitation to potentially emerging weed seeds should amplify the effect of microsite limitation on annual weed seedling recruitment. Research in the area has shown that emergence of weed species will cease on days where soil water potential falls below threshold values specific to each species (Forcella, 1998).

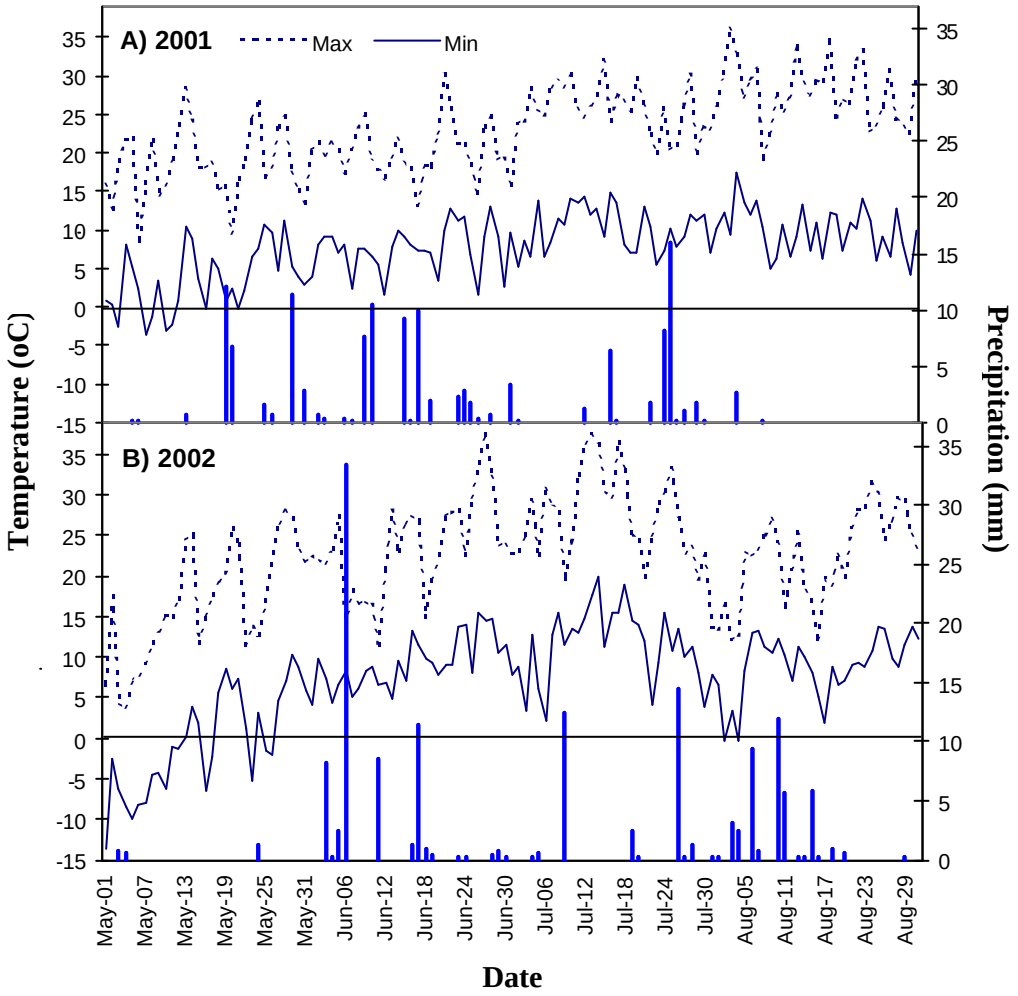

Figure 5.1: Growing season precipitation and temperature for Scott, Saskatchewan in 2001 and 2002.

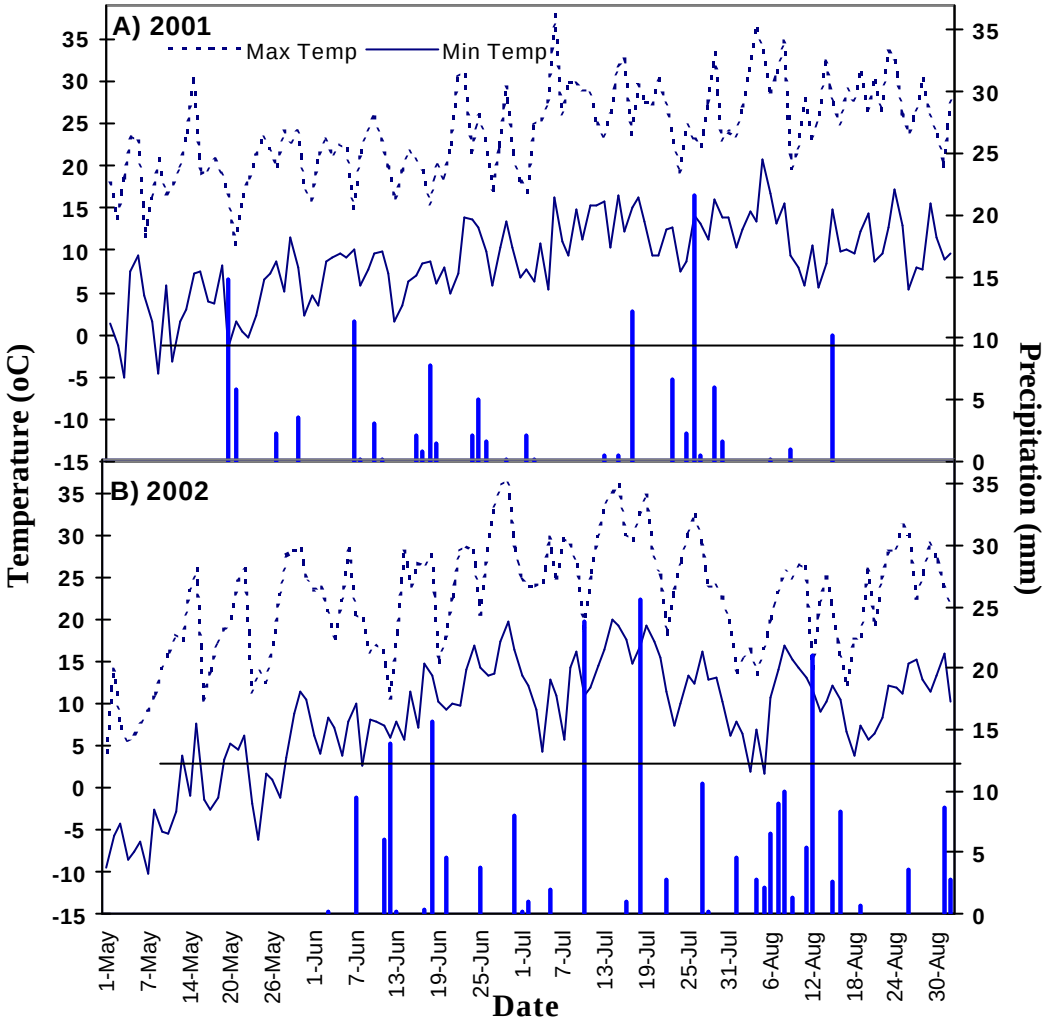

Figure 5.2: Growing season precipitation and temperature for Kernen, Saskatchewan in 2001 and 2002.

5.3.2 Cumulative Seedling Recruitment

Analysis of variance indicated the only consistent influence across all locations and years on the cumulative percent seedling recruitment was seed density (Table 5.1). In both years, Kernen was the only location to illustrate both a significant effect of tillage and a tillage-by-species interaction on percent seedling recruitment (Table 5.1). For Scott in both years, the strongest influences on seedling recruitment are density and the species-by-density interaction (Table 5.1).

Table 5.1: ANOVA of percent seedling recruitment (square-root transformed data) of green foxtail, wild oat, and wild mustard at densities of 20, 100, 500, 2500, and 12,500 weed seeds m^{-2} in conventional (chisel plough) and zero-tillage systems for Kernen and Scott, SK in 2001 and 2002.

	Kernen 2001		Scott 2001		Kernen 2002		Scott 2002	
Effect	**F-value**	**P-value**	**F-value**	**P-value**	**F-value**	**P-value**	**F-value**	**P-value**
Tillage	52.57	0.00	0.96	0.33	4.31	0.04	0.33	0.57
Species	37.25	0.00	10.53	0.00	39.00	0.00	1.61	0.21
Density	14.18	0.00	19.68	0.00	12.35	0.00	5.89	0.00
Tillage*Species	4.64	0.01	0.69	0.50	3.31	0.04	1.35	0.27
Tillage*Density	0.68	0.61	0.58	0.68	0.63	0.65	0.08	0.99
Species*Density	1.71	0.11	3.16	0.00	6.47	0.00	2.85	0.01
Tillage*Species*Density	0.58	0.79	0.42	0.91	1.49	0.17	0.42	0.91

Overall, when species were combined, increasing the seeding density resulted in decreased percent seedling recruitment for all locations (Figure 5.3). Kernen had higher levels of seedling recruitment at all target seeding densities, likely due to an overall marginally higher precipitation level than Scott for both growing seasons (Figure 5.1 and 5.2). Variability was quite high for this experiment, but trends indicated green foxtail had the highest seedling recruitment percentage of the species, particularly in the higher densities for Kernen in 2002 and Scott in 2001 (Figure 5.4). In all locations and years, wild oat exhibited a large decline in seedling recruitment from the 20 to 500 seeds m^{-2}, declining from 74 to 20% in Kernen, 93 to 31% in Scott 2001, and 90 to 45% in Scott 2002 (Figure 5.4). Only Scott in 2002 exhibited a further decrease in seedling recruitment for wild oat from the 500 to 12,500 seeds m^{-2} seeding rate (Figure 5.4). Overall, the lower densities had a greater percentage of seeds successfully recruiting, perhaps indicating a greater proportion of seeds were situated in favourable microsites. The higher densities, particularly for wild oat, although exhibiting relatively high seedling recruitment, had a greater proportion of seeds not recruiting, indicating seedling recruitment may have been restricted by the availability of microsites. The influence of microsite limitation appears to develop at seedbank densities of 2500 weed seeds m^{-2} and greater when all species were combined (Figure 5.3). Depending on the year and location, the level where microsite limited recruitment became more important based on a significant reduction in percent seedling recruitment differed, particularly for green foxtail and wild mustard (Figure 5.4). A significant decrease in percent seedling recruitment would indicate that fewer weed recruited proportionately in the treatment indicating more influence of the microsite on weed seedling recruitment.

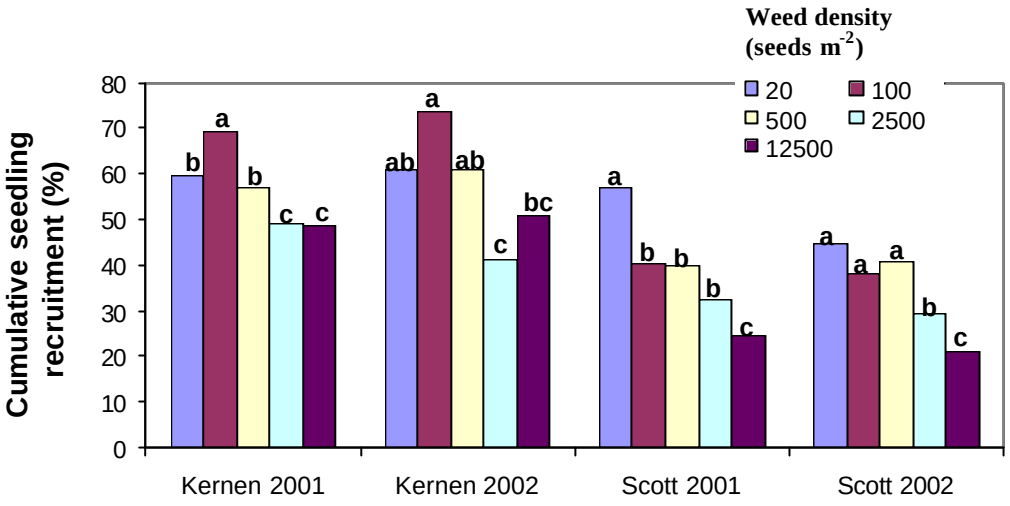

Figure 5.3: The effect of density on weed seedling recruitment (back-transformed data) for Kernen and Scott in 2001 and 2002 growing seasons. Letters indicate LSD (a=0.05) based on the transformed data in the analysis of variance within site-years.

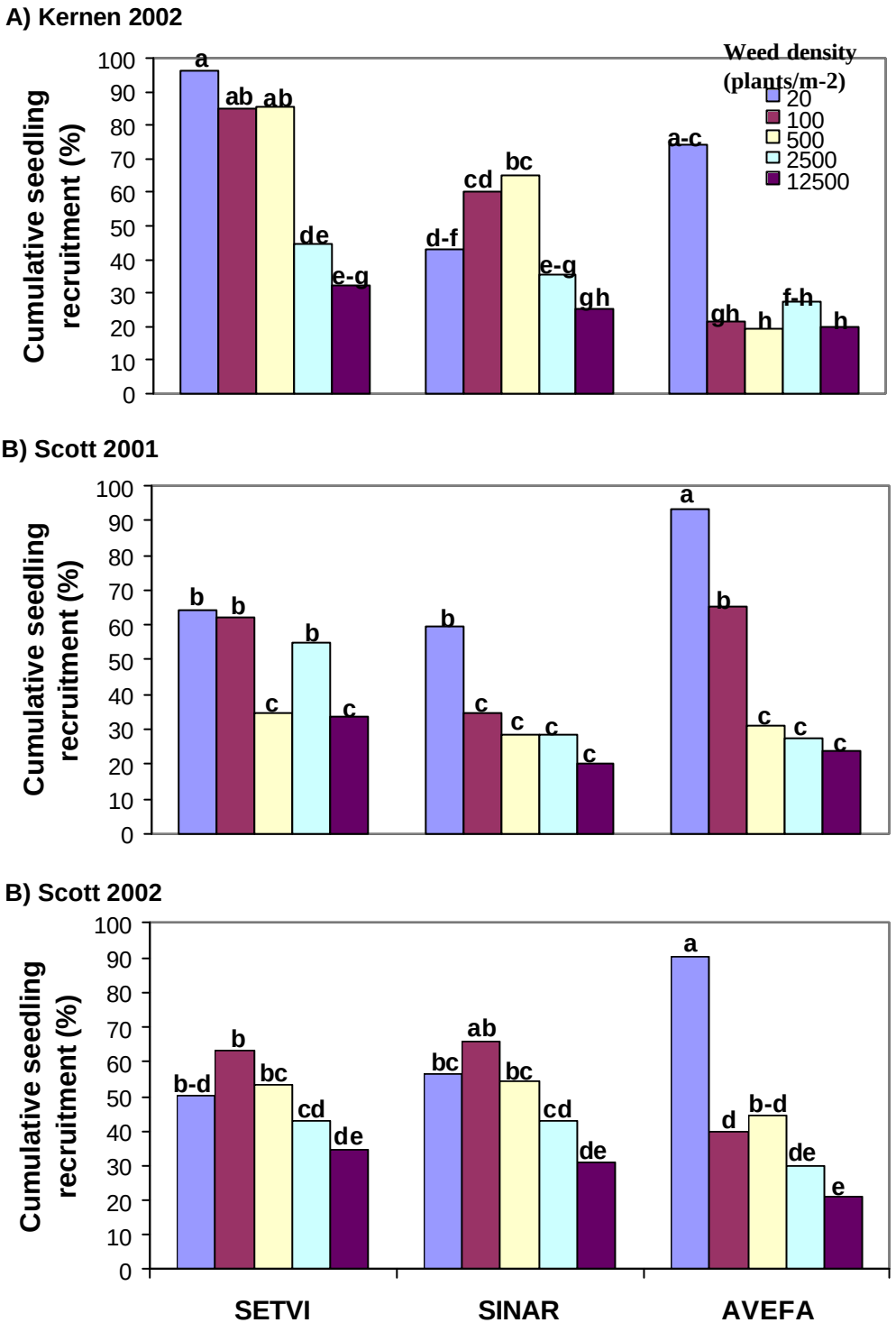

Figure 5.4: The significant effect of species by density interaction for three site years (Kernen 2002, Scott 2001, and Scott 2002) on weed seedling recruitment (back-transformed data). Letters indicate LSD (a=0.05) based on the transformed data. SETVI, SINAR and AVEFA indicate green foxtail, wild mustard, and wild oat, respectively. Note: there was not a significant effect in 2001 for Kernen.

Seedling recruitment can be limited either by availability of seed or microsite suitability (Erikkson and Ehrlen, 1992). At lower seedbank densities seed limitation seemed to be the main influence on weed seedling recruitment, while the influence of microsite limited recruitment became more important as the densities increased. For microsite limited recruitment to be the only factor limiting weed seedling recruitment, no increase in total weed seedling recruitment can occur, meaning each additional seed added would result in no new recruit (Eriksson and Ehrlen, 1992). Microsite limitation was not the most important factor limiting recruitment at the higher densities because actual recruitment numbers increased at all densities (Table 5.2). There was a 3 to 8-fold increase in total weed seed numbers from the 2,500 to 12,500 seeds m^{-2} target densities depending on the species. This increase in total weed number was also observed from the 12,500 to 62,500 seeds m^{-2} densities increasing recruitment from about 3000 to 6000 for wild mustard and 4000 to 10,000 for green foxtail (Table 5.2). The actual increase varied by location, but at each location, the increase in weed seedling recruitment at each level was clearly evident (Table 5.2). The biological effect of the microsite on weed seedling recruitment was not as significant as seed limited recruitment. Disregarding the low weed density of 20 plants m^{-2}, trends in seedling recruitment indicated that green foxtail had the most stable seedling recruitment across all densities and the highest total weed population for all locations and years (Table 5.2).

Table 5.2: Means for the number of actual weed seedlings recruiting (back-transformed data) of SETVI, SINAR, and AVEFA at six seeding densities (20, 100, 500, 2500, 12500, and 62500 seeds m^{-2}).

	Seeding Density (viable weed seeds m^{-2})					
Species	**20**	**100**	**500**	**2500**	**12500**	**62500**
			Kernen 2001			
SETVI	16	83	266	1134	4612	11740
SINAR	14	33	143	328	2825	7793
AVEFA	16	65	195	830	4006	NA*
			Scott 2001			
SETVI	18	67	189	1418	4346	10029
SINAR	18	39	150	725	2567	5215
AVEFA	19	70	167	722	3038	NA*
			Kernen 2002			
SETVI	19	85	456	1161	4143	9553
SINAR	16	79	336	900	3148	6206
AVEFA	19	29	107	696	2472	NA*
			Scott 2002			
SETVI	16	79	317	1106	4331	9659
SINAR	17	74	298	1093	3879	6265
AVEFA	19	46	229	793	2621	NA*

SETVI, SINAR and AVEFA indicate green foxtail, wild mustard, and wild oat, respectively.
* AVEFA did not have a seeding rate of 62,500 seeds m^{-2} because of physical limitations in seeding.

Some potential explanations for this reduced seedling recruitment of wild mustard and wild oat at higher densities include seed exudates limiting recruitment or density dependent mortality before emergence. Seed exudates can have both an allelopathic and autotoxic effect on seedling recruitment. Seeds can contain many allelopathic compounds, including sesquiterpene lactones, caffeic, vanillic, p-coumaric,

anisic, p-hydroxybenzoic, chlorogenic, and ferulic acids that may have inhibitory effects on germination (Hilhorst and Karssen, 2000). The knowledge on potential allelopathic compounds excreted by the species utilized in this experiment is limited. Increased surface area of the wild mustard cotyledon in comparison to wild oat and green foxtail may restrict germination at higher densities while the larger seed of wild oat may have restricted seedling recruitment due to increased H_2O usage by the larger seeded species and movement of the wild oat into a dormancy state (Murdoch and Ellis, 2000). Seeds can be kept in enough environmental stress to prevent germination and forced into a dormant state or in a quiescent state, including shortage of water, low temperature and poor aeration (Harper, 1977; Murdoch and Ellis, 2000). Although microsite limitation may play a factor in green foxtail recruitment, it appears that the impact of microsite limitation in arable agriculture is less important for green foxtail than wild oat and wild mustard. The overall size of the seed may influence the ability of a species to recruit. The size of a green foxtail microsite allows it to recruit from a wide range of locations, while wild oat and wild mustard are limited due to the size and shape of the seed. This ability of green foxtail to have a plastic response to weed seedling recruitment corresponds with the observations made in the weed survey where green foxtail had relatively high emergence at all landscape positions and equivalent seedling recruitment under zero-tillage and conventional tillage systems (Chapter 3). Green foxtail was least affected by density as well (Chapter 5) for successful weed seedling recruitment. With the inherent ability to emerge under a broad range of both landscapes, tillage systems, and densities, green foxtail remains a major weed in arable agriculture.

Tillage affected the cumulative seedling recruitment of the three species in Kernen for both years, but not in Scott (Table 5.1). Wild oat seedling recruitment was

not affected by tillage, while wild mustard had increased seedling recruitment in the zero-tillage treatment in Kernen (Fig. 5.5). Green foxtail had the highest seedling recruitment in zero-tillage in 2001 at Kernen, but no difference in 2002. Regardless of tillage, green foxtail had over 60% seedling recruitment (Figure 5.5). The increase in seedling recruitment under no-till systems for wild mustard and green foxtail in Kernen 2001 is contrary to other weed seedling recruitment studies where tillage can increase germination 1.5 to 3-fold (Peters, 1991), or a 6-fold increase for green foxtail alone (Mulugeta and Stoltenberg, 1997).

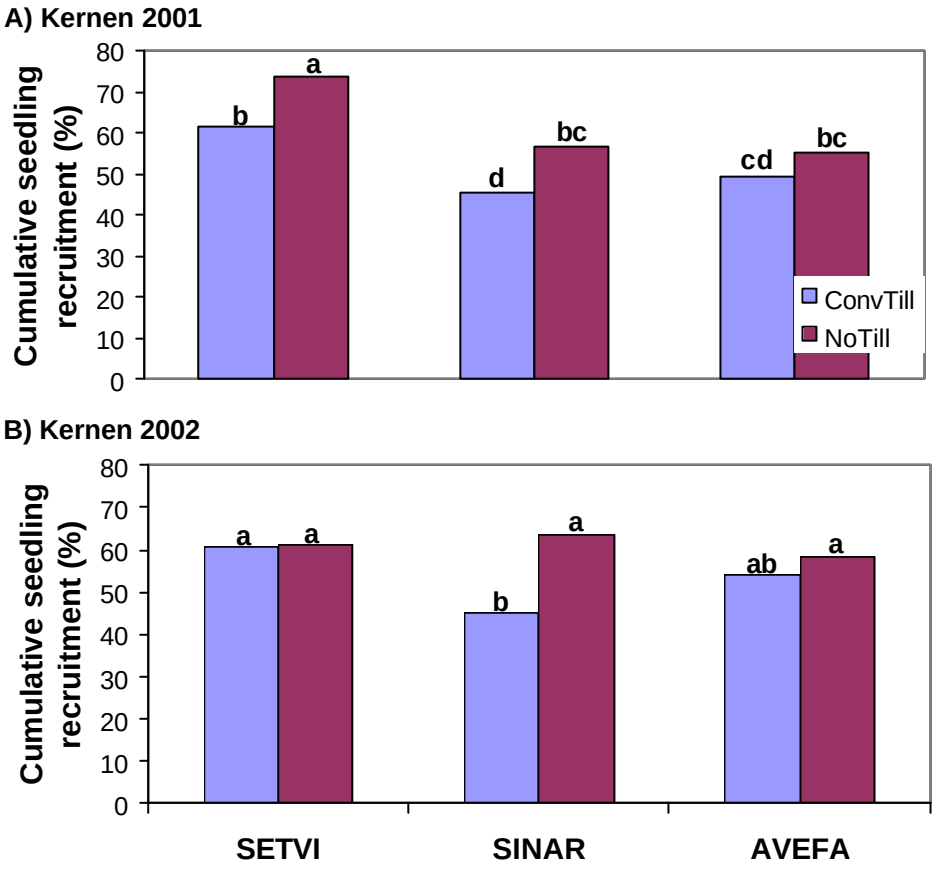

Figure 5.5: The effect of species by tillage system for Kernen on weed seedling recruitment (back-transformed data). Letters indicate LSD (a=0.05) based on the transformed data. Note: there was not a significant effect for Scott. SETVI, SINAR and AVEFA indicate green foxtail, wild mustard, and wild oat, respectively.

This experiment does not mimic normal cropping practices and utilized an introduced rather than a natural seedbank, as we were more interested in the initial density and not the cropping system. Application of weed seeds was not performed in the fall when annual weed species would typically disperse their seeds, but just prior to seeding when there would be a very limited chance of death in the zero-tillage system by predation, desiccation and other external factors. Seed predation in zero tillage systems can have a 32% decrease in comparison to 24% decrease in weed seed population under a chisel plough systems (Croman et al., 1999). The results in this experiment were similar to the results found in Derksen et al., 1994, 2002), where tillage did not affect total weed populations.

The differences between the locations for weed seedling recruitment are perhaps due to seeding equipment as the 20 cm row spacing in Kernen disturbed a greater portion of the seedbank than the 25 cm row spacing at Scott. The seeding implement used at Kernen also had the fertilizer applied by a disc opener applied between each row and consequently, the soil was disturbed every 10 cm. Fertilizer was side banded at Scott with no disturbance between the 25 cm row spacing. A greater portion of the field remained untouched with 25 cm row spacing than the 20 cm row spacing seeder. The disc openers disturbed a smaller portion of the seed bed for each opener, but if calculated as 5 cm on either side of the hoe drill used in Scott was disturbed and only 2.5 cm for the disc drill used in Kernen, the total seed bed utilization for Scott was 40% while the seed bed utilization at Kernen was 50%. Increased seeds on the soil surface, particularly at Scott, could have resulted in greater mortality of the weed seeds in the no-till system before recruitment could occur (Anderson et al., 2002), thus minimizing the

effect of tillage on seedling recruitment at Scott. Because the weed seeds were at the surface in the zero-tillage fields, the disturbance by seeding, particularly at Kernen, could move the weed seeds just under the soil surface where almost any amount of moisture could result in emergence as the majority of emerging weeds in either zero-tillage or tillage fields comes from close to the surface (Du Croix Sissons, 2000). In addition, for the species used in this experiment, wild mustard had lower emergence at 6-7 cm deep even at a field capacity soil moisture content with marginal decreases for wild oat and green foxtail in a recent recruitment experiment (Boyd and Van Acker, 2003).

In agriculture soils, the total available microsites change with the availability of resources within the soil profile. Consequently, the total microsites possible within the soil profile for weed seedling recruitment may not be the limiting factor, but the change in the total available microsites at the time of seedling recruitment due to the availability of resources. Early in the spring, availability of resources may have limited recruitment, and in particular the available moisture at the time of seedling recruitment over the two growing seasons in this experiment. Following the spring window for seedling recruitment, further seedling recruitment is limited by dormancy, temperature restrictions on germination (Baskin and Baskin, 1998) if the seed is not able to recruit following the winter snowmelt that occurs in the early spring. These are inherent mechanisms for weed survival enabling the weed to germinate and grow only when potential reproduction is still probable.

In general, weed seedling recruitment was not as impaired by microsite limitation as originally expected. Even at the highest seedbank densities, percent

seedling recruitment was close to the maximum emergence percentage for agriculture seedbanks of 40%, as determined by Forcella (1992). At 12,500 plants m^{-2}, percent seedling recruitment ranged from around 20% to 35%. With all species combined, the range of weed seedling recruitment percentage from lowest to highest weed density is 55% to 35%. Using the lowest cumulative weed seedling recruitment percentages observed in the experiment (wild oat density of 12,500 seeds m^{-2} at Scott) with back-transformed data, 19.5% of weed seeds successfully recruited, which corresponds to a total weed infestation of over 2,400 wild oat m^{-2}. The average seedling recruitment is well above typical recruitment numbers observed in the field of 9.0% to 28.1% (Dessaint et al., 1997). Natural seedbanks exhibit considerable dormancy. In this experiment, weed seedbank densities were based on viable weed seeds m^{-2}, which inflated weed seedling recruitment from the seedbank in comparison to natural systems. Nonetheless, results of this experiment indicated the relative lack of importance that microsite limitation had on germination and emergence. The microsite concept may still have importance for dormancy and survival of a species under different management practices as predation and dormancy are both major factors (Harper, 1977) that were not analyzed by this experiment.

A regression analysis was performed to examine the effect of percent seedling recruitment on the natural log of the density. There was a total overall decrease in the percentage of weed seeds recruiting as density increased indicating that the availability of microsites was a more important factor in weed seedling recruitment at higher seeding densities. A significant quadratic effect for wild oat and a significant linear effect for green foxtail and wild mustard indicated the cumulative percent recruitment decreased

as the density increased for each of the three species (Figure 5.6). Wild oat had the quickest reduction in percent seedling recruitment and thus had a greater number of seeds not recruiting due to microsite limitation at lower plant densities, but after the 500 weed seeds m^{-2} percent recruitment began to reach a constant level.

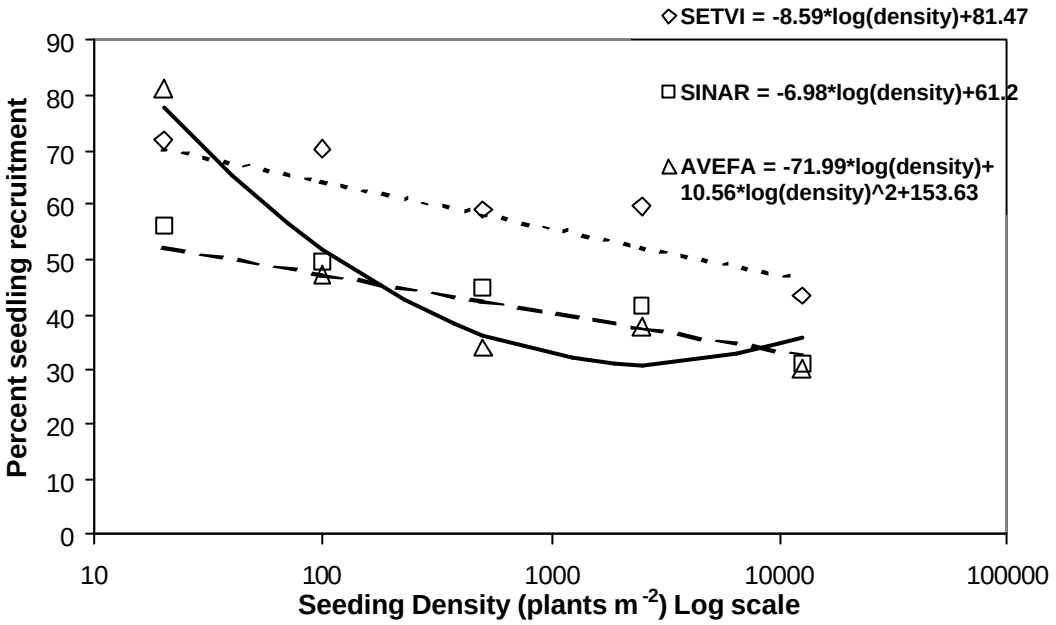

Figure 5.6: Regression analysis of cumulative percent seedling recruitment of SETVI, SINAR, and AVEFA combined site-years at five seeding densities (20,100, 500, 2500, and 12,500 weed seeds m^{-2}). SETVI, SINAR and AVEFA indicate green foxtail, wild mustard, and wild oat, respectively.

The increase at the highest density of 12, 500 weed seeds m^{-2} is merely an artifact of the quadratic equation and should indicate an asymptotic relationship, with percent seedling recruitment beginning to level off at 2,500 seeds m^{-2}. A linear relationship to the natural log of density illustrates that the percent seedling recruitment is leveling off as density increases and is an asymptotic relationship; an increase in

density results in only marginal decreases in percent emergence as weed seedbank densities increase. The quadratic effect of wild oat only emphasizes that wild oat reaches percent seedling recruitment asymptote at higher densities that may continuously decrease near zero as densities increase, most likely due to seed size limitations for resources necessary for germination to occur. The smaller seeded wild mustard and green foxtail require less resources for germination and emergence and will reach the percent recruitment plateau at higher densities. With a steeper slope, the effect of microsite limitation may be greater for wild oat than the other two species in the study.

5.3.3 Germination Index (Rate of Seedling Recruitment)

The germination index, a measurement for the rate of seedling recruitment was used to determine the relative agronomic impact that the speed of weed seedling recruitment would have on the crop. The faster a weed species germinates and emerges, the more impact it will have on the overall yield of the crop, and thus will have greater influence on the agro-ecosystem than a late emerging weed (Radosevich et al., 1997). Analysis of variance indicated that there was a significant effect of density, and species by density; however, mean comparisons using an LSD of a=0.05% in the mixed procedure of SAS resulted in no significant differences (Fig. 5.7).

Germination index increased for wild mustard as density increased, decreased for wild oat as density increased, and was relatively stable with some fluctuation between densities for green foxtail (Figure 5.7). The germination index for green foxtail was

unchanged between 100 and 12500 weed seeds m^{-2}, while each increase in seeding density for wild mustard resulted in a higher germination index (Figure 5.7).

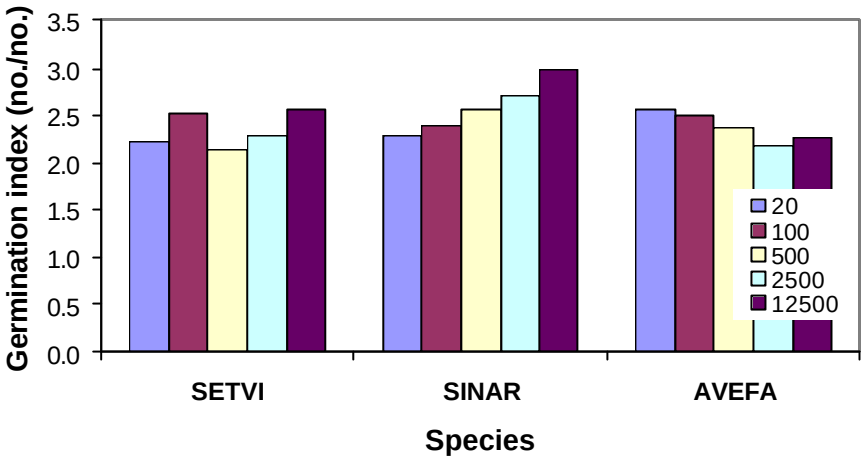

Figure 5.7: The effect of species and seeding density on the germination index for three annual weed species. Note: there were no differences based on the LSD (0.05), although analysis of variance indicated a significant effect at a level of p=0.05. SETVI, SINAR and AVEFA indicate green foxtail, wild mustard, and wild oat, respectively.

Late emerging weeds in the higher densities would allow for a decrease in rate of seedling recruitment as densities increase. The larger seed of wild oat may have allowed it to withstand some desiccation after germination before death occurred as larger seeds tend to be more resilient to stress and ultimately displace smaller seeded individuals in nature (Eriksson, 2000). Between these species, wild oat seedling recruitment was least affected by density, which could be one indication that wild oat microsite was less resilient at all densities to the stresses of growth and development experienced in 2001 and 2002. At the higher densities, increased intraspecific competition for moisture and other nutrients may have inhibited late-season seedling recruitment. With densities greater than 2,500 seeds m^{-2}, weed seeds may be close enough together to experience

competition for resources almost immediately after germination but prior to emergence. In this experiment with densities greater than 2,500 seeds m^{-2} for wild mustard and 12,500 m^{-2} for green foxtail, competition for resources and water prior to emergence may have prevented some seeds from germinating or emerging, particularly those seeds that did not germinate within the first couple of days. At higher densities, perhaps only the weed seeds that germinated first emerged and the weed seeds that germinated later, did not successfully emerge from the soil surface, thus not successfully recruiting.

5.3.4 Biomass and Seed Production

Analysis of variance indicated significant effects for species and species by density (Table 5.3). The differences in species are expected, as the three species have different growth characteristics and wild oat ultimately had the highest biomass production of the three species (Figure 5.8). Biomass production indicated the law of final constant yield, with biomass production reaching a peak for almost all the species at a rate of 2,500 weed seeds m^{-2} with no significant difference between the upper two densities for all species (Table 5.4). The low densities of 20 and 100 weed seeds m^{-2} resulted in low biomass and potentially low seed production for all weed species. Any higher density than this will result in high reproductive allocation and potential problems in future years by weed seed return into the weed seedbank. Even at 100 weed seeds m^{-2}, weed seed return could prove problematic for future years and weed control should be performed for all species. In addition, wild mustard reached its peak biomass at a lower density than wild oat or green foxtail. A density of 500 weeds seeded m^{-2} did not result in significantly lower biomass production than the highest seeding density (Table 5.4)

indicating lower densities can result in more significant yield impacts than equivalent densities of wild oat and green foxtail. High biomass production at lower weed densities indicates the importance of removing as many weeds as possible from a field. It is observed that even at low weed densities a large biomass production has the potential of returning high weed seeds into the weed seedbank resulting in future seedling recruitment problems. Weed seedling recruitment is both a function of the availability of weed seeds and the availability of microsites. Increasing weed production in one year can affect the total weed population in subsequent years as dormancy and microsite requirements are filled in subsequent years. Reducing the total number of weeds in a field remains an important factor in limiting weed seed production and will thus decrease the availability of seeds in subsequent years disrupting weed seed production will eliminate the need to examine microsite limitation due to availability of seed.

Table 5.3: ANOVA of biomass yield (g m^{-2}) of green foxtail, wild oat, and wild mustard at densities of 20, 100, 500, 2500, and 12,500 weed seeds m^{-2} in conventional (chisel plough) and zero-tillage systems for 2001 data compiled from both Kernen and Scott, SK.

Effect	F-value	P-value
Tillage	1.22	0.35
Species	3.54	0.16
Density	74.00	0.00
Tillage*Species	0.41	0.70
Tillage*Density	0.55	0.70
Species*Density	3.48	0.03
Tillage*Species*Density	1.25	0.35

Table 5.4: Cumulative biomass production (g m^{-2}) of three annual weed species (green foxtail, wild mustard, and wild oat at five seeding densities (20, 100, 500, 2500, 12500 plants m^{-2}) at Kernen, Saskatchewan in 2001.

Density (plants m^{-2})	SETVI	SINAR	AVEFA
20	5.55e	8.10e	15.17de
100	17.79de	13.02de	25.88de
500	33.83cde	51.77bcd	76.34b
2500	69.79bc	70.93bc	132.87a
12500	88.49b	82.34b	145.28a

a-e Letters indicate LSD between and within species (a=0.05).
SETVI, SINAR and AVEFA indicate green foxtail, wild mustard, and wild oat, respectively.

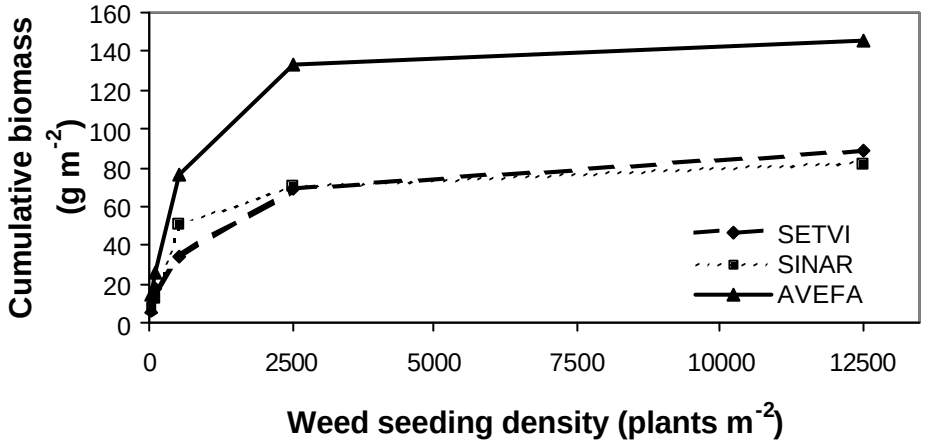

Figure 5.8: The effect of density on the biomass production of green foxtail, wild mustard, and wild oat for combined Kernen and Scott, SK in 2001. SETVI, SINAR and AVEFA indicate green foxtail, wild mustard, and wild oat, respectively.

5.4 General Conclusions

Weed seedling recruitment appeared to be more limited by the availability of seeds within the soil profile than the availability of microsites because each additional weed seed addition to the weed seedbank there is an increase in total weed seedling recruitment. For microsite to have a true effect on weed seedling recruitment, each

additional weed seed would result in no additional weeds being recruited in the landscape, which was not evident at any increase in density in this experiment. Statistically, there is an effect of microsite due to a decrease in total weeds recruiting proportionately at each density increase, but there is a seed limitation at each density observed in this experiment. Typical agricultural practices result in non-limiting resources for crop production, but at the site of the microsite these resources may limit the ability of a weed to recruit within the time of opportunity. Although non-dormant weeds were seeded into the experimental area, the time available for germination and emergence to proceed may have been restricted by the availability of resources at the microsite level for all weed seeds to successfully recruit. Consequently, the overall weed seedling recruitment was both a function of the availability of seed as well as the availability of resources at the specific microsite location where the weed seed was present. Statistically, percent recruitment decreased with density, which indicates that fewer seeds found suitable conditions for germination and recruitment; however, the absolute number of weed seedlings recruiting increased continually at each incremental density increase. This impact of density is definitely not agronomically significant and the use of the microsite concept in an agricultural setting is limited. Factors that prevent seedling recruitment and establishment, such as dormancy, hazards, and availability of resources should be examined with respect to the availability of microsites within agricultural soils to further increase our knowledge of weed seedling recruitment.

Of the three species examined in the experiment, green foxtail had the highest seedling recruitment among both tillage systems and was the least restricted by seed density. The ability of green foxtail to exhibit high seedling recruitment in a broad

range of environments has been well illustrated by the high recruitment under both tillage regimes used in this experiment.

6. General Discussion and Conclusions

The degree of microsite versus seed limited recruitment was examined extensively for a number of annual weed species. From the survey results, it was evident that N availability had little effect on weed seedling recruitment across the three landscape positions examined. Tillage had a significant influence on the ability of weed seedlings to recruit from the indigenous seedbank with early season recruitment always being higher in the tilled soil in comparison to the zero-tillage treatments. The question remained whether the tillage treatment increased the absolute number of available microsites or simply removed some of the barriers preventing seedling recruitment from occurring. The tillage treatment in the spring may have decreased the number of hazards or changed the dormancy characteristics of the seeds in the seedbank, which are two essential aspects of the microsite concept (Harper, 1977). If the tillage treatment increased the position of the viable non-dormant seeds within the seedbank, this would have indicated that tillage has an effect on weed seedling recruitment by placing the weed seeds into favourable microsites within the soil profile. As well, tillage may have increased the absolute number of microsites or increased the total viable seed population by preventing mortality prior to germination or breaking dormancy for the seeds examined in this experiment.

In addition, there were indications of habitat differentiation for weed recruitment patterns. Preferential recruitment in the lower landscape positions by wild oat and cleavers suggested these were hydrophilic species, which needed greater moisture to germinate and emerge whereas kochia and Russian thistle exhibited xerophytic or stress

resilient properties by preferentially recruiting in the upper landscape positions suggesting the level of moisture limitation was lower for these species. Green foxtail exhibited no difference between the upper and lower slope positions, recruiting under a broad range of moisture and environmental conditions suggesting a generalist recruitment pattern. Questions arising from these results suggest that removing moisture as a limiting factor for wild oat and cleavers would allow the species to preferentially recruit from any location; however, without examining the seedbank in detail, the most likely reason the weeds recruited preferentially in contrasting slope positions was due to their overall abundance in the seedbank. In a pure seedbank, with known populations of individuals, would seedling recruitment of individual species result in habitat differentiation of the weed species? Unfortunately, the lack of a potential stress resilient specialist species such as kochia or Russian thistle due to seed availability for the landscape irrigation experiment resulted in inconclusive results for the classification of species into specific categories.

Questions arising from the survey results coincided with the examination of specific trials focusing on the overall landscape effect and moisture effect of seedling recruitment of wild oat, green foxtail, and wild mustard as well as the influence of seed versus microsite limitation of these species under two tillage systems. Although hypothesized that the upper landscape positions would result in a greater increase in overall seedling recruitment with an irrigation treatment, results indicated that each landscape increased recruitment equally with irrigation while the upper landscape positions never reached equivalent seedling recruitment for wild mustard and wild oat, two hypothesized hydrophilic recruitment specialists. Green foxtail ultimately did not significantly increase seedling recruitment under irrigation emphasizing its ability to

recruit under the broadest range of conditions experienced in the experiment. In addition, green foxtail always had nominally the highest seedling recruitment of the species under all experimental conditions.

This experiment also suggested that although seedling recruitment may be an important first step in development of a plant, it might not be as important for patch dynamics than establishment, survival, and development to maturity. Green foxtail produced equivalent biomass production across all slope positions while wild oat and wild mustard had significant decreases from the lower to mid and upper landscape positions for overall biomass production. This ability of green foxtail to produce evenly across the landscapes may allow it to increase in overall abundance in the weed seedbank across all landscapes, while wild mustard and wild oat increase by reproduction only where favourable to do so. The overall impact of the microsite on weed seedling recruitment may in fact be very minimal in arable agriculture if fertilizer is optimized, and the seedbed in spring is relatively optimal for moisture and temperature. Perhaps regardless of location within a landscape, any species can recruit, but only the hardy, dominant species ultimately survive.

To further examine this influence of microsite versus seed limitation, the same three weed species were seeded at a wide range of densities to examine the influence of seed and microsite on seedling recruitment. Opposite to the survey results, there was no effect of tillage for a known seedbank of weed seedlings. This suggests that the aspects of microsite limitation that are most important in agricultural systems may be freedom from hazards such as insects or diseases that attack the seed or the movement from dormant to non-dormant seeds that may occur by a tillage application. Additionally, this trial was implemented in the spring perhaps removing some of the additional hazards

observed in zero tillage systems such as freeze-thaw events on the surface, which would affect fall-dispersed seeds. Ultimately, one can determine that when a known or artificial set of viable seeds is seeded, tillage has no effect.

Decreases in percent weed seedling recruitment in this experiment were quite small and were only observed at extremely high seed densities. On the other hand, this experiment suggested that the ability to establish and survive to maturity was perhaps more important than seedling recruitment for plant success as for all species, as the biomass was close to reaching its peak production at 500 weed seeds planted m^{-2}. Again, this suggests recruitment is not the most essential process for weed patch development.

Although present in arable agriculture, microsite limitation has a very limited influence on the spatial distribution of weeds across a landscape. Seedling recruitment is an essentially first step in establishment of a species into a new landscape, but the ability of that species to establish itself and survive until reproduction will determine whether a species will dominate within a spatial area. The ability of a species to recruit and produce seed across a wide range of landscapes, moisture regimes, and tillages will allow that species to become a widespread weed, while other weeds develop in patches due to their ability to recruit and ultimately establish themselves in specific locations. Wild oat, although present in all landscape positions, can dominate a lower landscape position because of its ability to produce seed and increase its total population in a seedbank. The requirements of a microsite can be fulfilled across a wide range of landscapes, but other species may have greater establishment abilities and prevent a specific species from increasing in seedbank proportion.

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